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Life-Forms of Kentucky Flowering Plants

DOROTHY GIBSON

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ABSTRACT: A study was made of the vegetative structures of all reported species of Kentucky flowering plants, in order to determine the percentage distribution of species among the assigned life-forms, and in hope of stimulating further research in this field. Species were tabulated according to duration, life-form (Raunkiaer) and extended scheme (Turrill), and the biological spectrum obtained from summarizing these tabulations was compared with Raunkiaer's "normal" spectrum and the spectra of other known regions. In addition to reflecting Kentucky's high percentage of hemicryptophytes, the study reveals considerable variation in growth habit behavior within a species, indicates the usefulness of such criteria in the determination of plant communities, and points up the need for detailed studies of community relationships.

Life-forms are assumed to be the result of each plant's evolutionary morphological adjustment to its environment. A variety of vegetative structures have developed, by natural selection, enabling plants to function in harmony with environmental changes. This study attempts to establish the kinds and degrees of protection afforded the perennating buds of Kentucky plants during the unfavorable season; to determine the percentage distribution of species among the assigned life-forms, and to compare the resulting biological spectrum with Raunkiaer's "normal" spectrum and the spectra of other regions.

The historical review of physiognomic and epharmonic systems of classification outlined by Sr. Elizabeth Seton MacDonald in her paper, "The life-forms of the flowering plants of Indiana" (1937), adequately presents accounts of the various systems and methods and will therefore not be repeated here. Raunkiaer's system, based upon the position on the plant of rejuvenating organs, has been followed, and the species are classified according to Turrill's "extended scheme" of duration and external characteristics.

When this study was initiated, it was realized that more than one climatic type often occurs within the boundary of a state. However, it was hoped that a series of such state studies would at least show the changing form-trend or gradient as controlled by temperature, atmospheric precipitation, and soils. The resulting spectra of the same general climate types do reflect the same broad patterns of life-form types (Tables II and III), supporting the premise that there is a correlation of life-forms and environments. However, the spectra are most useful in bringing out features for investigation as they point up the facts that one form cannot be singled out as indicative of an

environment, and that life-forms are in part the result of the floral composition of the unit being studied, and of the history of that floral unit. The complexities of such relationships cannot be shown by simple comparative lists, and I am convinced that only by many unit studies in the field, leading to a series of zone studies based on dominant species and frequency data as suggested by Cain (1945), can the situation be accurately expressed. Although this approach is unfortunately impracticable at present for many, I believe it is the only way that we can eventually arrive at a true picture of edaphic conditions and prevailing phytoclimates, as well as original natural areas. (In this connection it is hoped that collectors will realize that specimen labels containing more information as to dominant plants in the associations of each habitat would permit the construction of more useful spectra.)

As this study progressed, it became increasingly apparent that more variation in growth habit behavior exists than is generally known or has been reported. A species may have more than one life-form in accordance with habitat, age, or other factor. A specimen of *Stellaria pubera* (usually appearing as a chamaephyte) collected by Dr. E. Lucy Braun was an upright proto-hemicryptophyte; *Cirsium vulgare,* wintering as an obvious semi-rosette, also produces root-buds on a horizontal rhizome. *Arabis perstellata,* a semi-rosette type, was found by Braun (1956) to be perennial by means of a slowly elongating central axis. Hemicryptophytes which are able to produce runners or stolons do not always do so. Eight species of *Viola* which had produced runners were collected in Kentucky and were so reported from Connecticut by Ennis (1928). However, five of these eight species collected in Indiana were found to be without runners (MacDonald, 1937). Some plants behave variously as annuals, biennials, or even triennials. *Sedum pulchellum,* an obviously perennial chamaephyte in limestone soil in Edmonson County, Kentucky, appears in Jessamine County, also in limestone soil, as a biennial (*Braun 1984* and *920,* private collection).

Factors other than light or temperature may be much more important in the establishment of plant associations in various habitats. The fact that many geophytes, especially among the monocotyledons, bloom very early before shade is furnished by the forest environment, indicates that the forest habitat is necessary for other reasons — perhaps symbiotic fungal relationships, as in the case of the later blooming *Monotropa hypopithys,* a root-bud geophyte, which is also an epiparasite by way of a mycorhiza which is in turn dependent on forest tree roots (Björkman, 1959). A study of life-forms emphatically points up the need for detailed study of community relationships. It is not enough to know that certain synusiae exist in certain habitats — we need to know why they are where they are and the answers must lie in many carefully planned seasonal field studies of smaller ecological units.

Specific names used in this study are essentially those listed by Braun (1943) and, with certain exceptions, McFarland (1942). The

species omitted are those represented by specimens which could not be checked, as specimens lost when fire destroyed the herbarium of the University of Kentucky were not all duplicated in other herbaria. When a name has been reduced to synonymy since these lists appeared, and when the later revision is generally recognized, the revised nomenclature has been used. A few species reported since 1943 which were available for examination have been added and are annotated. Previously unreported species are also annotated and are indicated as new state records by double asterisks. Naturalized species (indicated by a single asterisk), which are included in the distributional summary in Table I, are also summarized by family, following the systematic list (Table VI). Species which have been observed to vary in duration or form are included in parentheses in the summaries preceding each group. In addition, Table V was prepared to compare the percentage distribution of woody types, parasites and saprophytes, aquatics, and herbaceous twining plants. The following symbols are used in the tabulations and summaries:

B. T — Tree. Sh — Shrub. (4) — Perennial. (2) — Biennial. (1) — Annual.

C. Ph — Phanerophytes:
- MM — Mega- Meso- Phanerophytes (Bud-heights 8 to 30 m or more)
- M — Micro-Phanerophytes (Bud-heights 2 to 8 m)
- N — Nano- Phanerophytes (Bud-heights below 2 m)

Ch — Chamaephytes

H — Hemicryptophytes
- Hp — Proto-Hemicryptophytes without runners.
- Hs — Semi-Rosette without runners.
- Hr — Rosette without runners.
- Hpr — Proto-Hemicryptophytes with runners.
- Hsr — Semi-Rosettes with runners.
- Hrr — Rosette with runners.

Cr — Cryptophytes
- G — Geophytes
  - Grh — Rhizome
  - Gst — Stem-tuber
  - Grt — Root-tuber
  - Gb — Bulb
  - Gr — Root-bud
  - Gp — Root-parasites
- HH — Helo-, Hydrophytes

Th — Therophytes

S — Stem Succulents

E — Epiphytes

D.
1. Evergreen tree.
2. Deciduous tree.
3. Evergreen shrub.
4. Deciduous shrub.
5. Woody liana or sprawler.
7. Plant with spines, thorns, or strong prickles.
9. Perennial herb, or sub-shrub, partially woody at base, with aerial parts dying back but not to ground level.
10. Grasses and grass-like plants.

11. Rush and sedge forms with suppressed leaves.
12. Perennial herbs and subshrubs with runners, or sprawling, ascending, or herbaceous or suffruticose stems.
14. Rosette plants.
15. Herbaceous twining plants generally dying down each year.
16. Perennial herbs dying down yearly with perennial buds on more or less thick stock at ground level.
17. Geophytes.
18. Annual herbs.
19. Hydrophytes.
20. Parasites and saprophytes.

(NOTE: Categories 6 — shrubs, and 13 — cushion plants, were omitted for Kentucky plants.)

TABLE I.—Distributional summary of native and naturalized species

			Duration				
	Fam.	Spp.	T	Sh	(4)	(2)	(1)
Native and naturalized	129	1846	141	174	1149	86	296
Naturalized	37	226	8	9	75	32	102
Native	92	1620	133	165	1074	54	194

	Life-form				
	Ph	Ch	H	Cr	Th
Native and naturalized	300	26	942	282	296
Naturalized	16	3	94	11	102
Native	284	23	848	271	194

In the systematic list, an entry of symbols representing life-form and duration will hold for all subsequent taxa in that family, unless a new entry appears.

Kentucky, an area of 40,598 square miles, lies approximately 38° N. latitude and 85° W. longitude, with altitude ranging from 275 feet to 4,250 feet. That part of the state in the physiographic province of the Interior Low Plateau (Fenneman, 1938) includes the western coal fields, the rugged escarpments of the Highland Rim (mixed deciduous forests, uplands of oak, hickory, and red cedar, pine-covered ridges),

TABLE II.—Biological spectrum of Kentucky, compared with the "normal" spectrum of Raunkiaer and available spectra of other regions

	No. of native spp.	Ph	Ch	H	Cr	Th
Connecticut (Ennis)	1453	15.0	1.9	49.4	21.7	11.7
Olympic Peninsula (Jones)	1015	11.0	6.0	52.0	22.0	9.0
Illinois (Hansen)	1909	15.5	1.6	50.2	19.8	12.9
Indiana (MacDonald)	1837	15.3	1.7	50.3	19.6	13.0
Kentucky	1620	17.6	1.4	52.6	16.6	11.8
Normal spectrum		46.0	9.0	26.0	6.0	13.0

the fertile bluegrass, and the karst regions to the south. The eastern section, in the Appalachian Highlands, includes part of the unglaciated Allegheny Plateau, and the mixed mesophytic forests of the Cumberland Mountains and the Cumberland Plateau. The mean annual temperature for the state is 56° F.; annual rainfall averages 45 inches, and there are normally about 180 days each year without frost.

In this favorable climate, Kentucky's native hemicryptophytes surpass those of Indiana and Illinois by over two per cent (Table II). The percentage of native phanerophytes, also more than two per cent higher than that of the neighboring states to the north, was to be expected. The prevailing temperature, humidity, and length of growing season favor these two groups, the herbaceous layer being controlled to some extent by the canopy layer. There is little doubt that during glaciation, the slopes and ravines of the forests along the northern boundary provided refugia for northern species, while the

TABLE III.—Comparisons of biological spectra of various regions, including introduced species

	No. of native and naturalized species	Ph (MM	Ph M	Ph N)
Cape Breton (Ennis)	637	4.3	3.7	6.1
Connecticut (Ennis)	1622	5.4	5.6	3.5
New York (Taylor)	1907	4.5	7.2	3.5
Illinois (Hansen)	2071		(13.9)	
Indiana (MacDonald)	2109	5.8	5.5	3.0
Kentucky	1846	6.3	6.8	3.2
Piedmont, N. C. (Oosting)	387		(29.7)	
North Carolina—Tenn., Smoky Mtns. (Cain)	1142	8.9	6.1	4.5
Alabama (Ennis)	2012	7.7	4.6	4.7
Mississippi (Ennis)	1724	8.9	4.6	4.2

	No. of native and naturalized species	Ch	H	Cr (G	Cr HH)	Th
Cape Breton (Ennis)	637	1.8	51.3	15.3	10.3	6.7
Connecticut (Ennis)	1622	2.0	49.4	12.6	7.7	13.5
New York (Taylor)	1907	5.3	33.3	20.2	11.7	13.0
Illinois (Hansen)	2071	2.0	47.5	(17.1)		14.4
Indiana (MacDonald)	2109	1.9	49.0	12.6	5.4	16.7
Kentucky	1846	1.4	51.2	12.4	2.9	15.8
Piedmont, N. C. (Oosting)	387	1.6	45.0	(11.3)		12.4
North Carolina—Tenn., Smoky Mtns. (Cain)	1142	1.7	52.1	15.1	......	11.5
Alabama (Ennis)	2012	3.1	47.8	12.8	4.3	14.4
Mississippi (Ennis)	1724	3.1	49.4	12.4	3.8	12.8

southern species were not displaced. The gray-brown, melanized forest soils which predominate are known for their productivity. Another factor to be considered is that many Kentucky counties have not been adequately collected, some are still botanically unreported, and a greater part of those which have been reported are now or were recently forest regions, favorable to hemicryptophytes.

The fact that Kentucky has a greater percentage of microphanerophytes (Table III) than the states to the north or to the south is understood when we take into account the number of large trees cut in lumbering operations. Also, shrubby plants appearing as nanophanerophytes to the north may here become small trees.

The chamaephyte percentage is only 0.2 per cent less than Illinois and 0.3 per cent less than Indiana. The Kentucky cryptophyte percentage, three per cent less than that of the two northern states, may be explained by pointing out the unusually low helo-hydrophyte count, which normally contributes one-third to one-half of the cryptophyte percentage (also see Table V). This is almost certainly incorrect, as very little collecting has been reported from the many aquatic and semi-aquatic habitats in the state.

The native therophyte population is 1.2 per cent less than that of Indiana and 1.1 per cent less than that of Illinois. When introduced species are included (Table III), the altered therophyte percentage, as expected, shows the greatest increase, surpassed only by that of Indiana. The only acceptable explanation for the high percentage of therophytes in Indiana seems to be that Indiana has been more completely collected and reported.

The Pteridophyte quotient (Pt.-Q.) of Kentucky, summarized in Table IV to express the ratio of spermatophytes to pteridophytes, is compared with spectra available for some other regions. Data for the Pt.-Q. spectra was obtained from McCoy's list (1937), with additions from lists prepared by McFarland (1942), Reed (1958), and Smith (1959). The very high Pt.-Q. of 1.26 per cent is probably due to the fact that the entire region has undergone less climatic change and less soil change during erosion cycles than adjacent regions. The humid

TABLE IV.—Pteridophyte-quotient (Pt.-Q.) of Kentucky and other regions

	Number of native species		
	Spermatophytes	Pteridophytes	Pt.-Q. Ratio
World	140,000	5,600	25:1
Laurentian (Marie-Victorin)	1,837	80	1.1
Connecticut (Raunkiaer)			1.3
Illinois (Hansen)	1,681	64	0.95
Indiana (MacDonald)	1,837	58	0.8
Kentucky	1,620	82	1.26
Alabama (Raunkiaer)			0.7
New Mexico (Raunkiaer)			0.3

TABLE V.—Comparisons of native woody types, aquatics, and parasitic plants

	Woody types	Aquatics	Parasites and saprophytes
Connecticut	15.0	8.5	....
Illinois	16.2	5.5	1.4
Indiana	16.5	6.2	.8
Kentucky	18.5	3.2	1.1

forest climax has existed since Tertiary times. Old and relatively undisturbed soils (mull humus of the forests, limestone and shale outcrops, and sandstone soils of plateaus and ridges) are much more favorable to a variety of pteridophytes than are eroded, or new soil types to the north or the alluvial embayment to the south.

Kentucky's diversified topography of mountains, plateaus, river bluffs, and "prairie" grasslands produces highly variable climax and subclimax communities. When this state flora has been completely collected and reported, serious studies of these complex and most interesting ecological compositions should be made.

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SYSTEMATIC LIST

SPERMATOPHYTA

Families: 129. A. Genera: 626. Species: 1,846. Varieties: 266.
B. T—141 (+6). Sh—174 (+4). (4)—1149 (+8). (2)—86 (+11). (1)—296 (+17).
C. MM—114 (+3). M—127 (+4). N—59 (+2). Ch—26(+1). H—942 (+1). G—230 (+1). HH—52 (+1). Th—296 (+6). S—1. E—1.
D. 1—13. 2—136 (+7). 3—16. 4—115 (+2). 5—49(+1). 7—71. 9—8. 10—314 (+1). 11—9. 12—23. 14—75. 15—16. 16—655 (+2). 17—202. 18—296 (+2). 19—30. 20—19.

GYMNOSPERMAE

Families: 2. A. Genera: 5. Species: 8. Varieties: 1.
B. T—7. Sh—1. C. MM—7. N—1. D. 1—6. 2—1. 3—1.

1. *Taxaceae*

A. Genera: 1. Species: 1. B. Sh—1. C. N—1. D. 3—1.

Taxus canadensis Marsh. B. Sh C. N D. 3

2. *Pinaceae*

A. Genera: 4. Species: 7. B. T—7. C. MM—7. D. 1—6. 2—1.

Pinus strobus L.	B. T	C. MM	D. 1
P. echinata Mill.			
P. virginiana Mill.			
P. rigida Mill.			
Tsuga canadensis (L.) Carr.			
Taxodium distichum (L.) L. C. Rich.	B. T	C. MM	D. 2
Juniperus virginiana L. var. *crebra* Gern. and Grisc.	B. T	C. MM	D. 1

ANGIOSPERMAE

Families: 127. A. Genera: 621. Species: 1838. Varieties: 265.
B. T—134 (+6). Sh—173 (+4). (4)—1149 (+8). (2)—86 (+11). (1)—296 (+17).
C. MM—107 (+3). M—127 (+4). N—58 (+2). Ch—26 (+1). H—942 (+1). G—230 (+1). HH—52 (+1). Th—296 (+6). S—1. E—1.
D. 1—7. 2—135 (+7). 3—15. 4—115 (+2). 5—49 (+1). 7—71. 9—8. 10—314 (+1). 11—9. 12—23. 14—75. 15—16. 16—655 (+2). 17—202. 18—296 (+2). 19—30. 20—19.

Monocotyledonae

Families: 19. A. Genera: 137. Species: 463.
B. Sh—5. (4)—393 (+1). (2)—(1). (1)—65 (+1).
C. M—5. N—2. Ch—1 (+1). H—223 (+1). G—133 (+1). HH—33 (+1). Th—64 (+1).
D. 1—6. 2—1. 3—2. 5—5. 7—5. 9—1. 10—314 (+1). 11—9. 12—1. 14—5. 15—6. 16—28. 17—104. 18—64. 19—15. 20—4.

1. *Typhaceae*

A. Genera: 1. Species: 2. B (4)—2. C. HH—2. D. 16—2.

Typha latifolia L.	B. (4)	C. HH	D. 16
T. angustifolia L.			

2. *Sparganiaceae*

A. Genera: 1. Species: 2. B. (4)—2. C. HH—2. D. 16—2.

Sparganium androcladum (Engelm.) Morong	B. (4)	C. HH	D. 16
S. americanum Nutt.			

3. *Potamogetonaceae*

A. Genera: 1. Species: 7. B. (4)—7. C. HH—7. D. 19—7.

Potamogeton americanus Cham. & Schlecht.	B. (4)	C. HH	D. 19
P. pectinatus L.			
P. diversifolius Raf.			
P. foliosus Raf. var. *macellus* Fern.			
P. panormitanus Biv.			
P. berchtoldi Fieber var. *tenuissimus* (Mert. & Koch) Fern.			
P. epihydrus Raf.			

4. *Najadaceae*

A. Genera: 1. Species: 2. B. (4)—2. C. HH—2. D. 19—2.

Najas guadalupensis (Spreng.) Morong	B. (4)	C. HH	D. 19
N. gracillima (A. Br.) Morong			

5. *Alismaceae*

A. Genera: 4. Species: 7. B. (4)—7. C. HH—7. D. 16—7.

Alisma subcordatum Raf.	B. (4).	C. HH	D. 16
Echinodorus radicans (Nutt.) Engelm.			
Lophotocarpus calycinus (Engelm.) J. G. Sm.			
Sagittaria graminea Michx.			
S. brevirostra Mack. & Bush			
S. latifolia Willd. var. *obtusa* (Muhl.) Wieg.			
S. longirostra (Mich.) J. G. Sm.			

6. *Hydrocharitaceae*

A. Genera: 2. Species: 2. B. (4)—2. C. HH—2. D. 19—2.

Anacharis canadensis (Michx.) Planch.	B. (4)	C. HH	D. 19
Vallisneria americana Michx.			

7. *Gramineae*

A. Genera: 57. Species: 182. B. (4)—130 (+1). (2)—(1). (1)—52.
C. N—1. Ch—(1). H—115. G—14. Th—52.
D. 10—182. 12—1. 18—52.

Arundinaria gigantea (Walt.) Chapm.	B. (4)	C. N (Ch)	D. 10
Bromus latiglumis (Shear.) Hitchc.	B. (4)	C. Hs	D. 10
B. purgans L. var. *laeviglumis* (Scribn.) Swallen			
**B. inermis* Leyss.	B. (4)	C. Hsr.	D. 10
**B. secalinus* L.	B. (1)	C. Th	D. 10, 18
**B. commutatus* Schrad. var. *apricorum* Simonkai			
**B. japonicus* Thunb.			
**B. arvensis* L.			
**B. sterilis* L.			
**B. tectorum* L.			
Festuca octoflora Walt. var. *tenella* (Willd.) Fern.			
**F. elatior* L.	B. (4)	C. Hs.	D. 10
F. obtusa Spreng.			
F. paradoxa Desv.			
Glyceria acutiflora Torr.			
G. septentrionalis Hitchc.			
G. melicaria (Michx.) F. T. Hubb.			
G. striata (Lam.) Hitchc.			
Poa chapmaniana Scribn.	B. (1)	C. Th	D. 10, 18
**P. annua* L.			
**P. compressa* L.	B. (4)	C. Hsr	D. 10
P. pratensis L.	B. (4)	C. Grh	D. 10
P. cuspidata Nutt.	B. (4)	C. Hsr.	D. 10

*_P. trivialis_ L.			
P. alsodes A. Gray	B. (4)	C. Hs	D. 10
P. nemoralis L.			
P. languida Hitchc.			
P. sylvestris A. Gray			
P. autumnalis Muhl.			
Eragrostis reptans (Michx.) Nees	B. (1)	C. Th	D. 10, 18
*_E. megastachya_ (Koel.) Link (Meade County—Davies, 1955. Univ. Louisville Herbarium)			
E. hypnoides (Lam.) BSP.			
E. capillaris (L.) Nees			
E. frankii C. A. Mey.			
*_E. pilosa_ (L.) Beauv.			
E. pectinacea (Michx.) Nees			
*_E. cilianensis_ (All.) Link			
E. hirsuta (Michx.) Nees	B. (4)	C. Hs	D. 10
E. spectabilis (Pursh) Steud.			
Diarrhena americana Beauv.	B. (4)	C. Grh	D. 10
Uniola latifolia Michx.	B. (4)	C. Hsr	D. 10
U. laxa (L.) BSP.			
*_Dactylis glomerata_ L.	B. (4)	C. Hs	D. 10
Melica mutica Walt.			
M. nitens (Scribn.) Nutt.			
Schizachne purpurascens (Torr.) Swallen			
Triodia flava (L.) Smyth	B. (4)	C. Hsr	D. 10
*_Agropyron repens_ (L.) Beauv.	B. (4)	C. Grh	D. 10
A. smithii Rydb.			
Elymus villosus Muhl.	B. (4)	C. Hs	D. 10
E. canadensis L.			
E. riparius Wieg.			
E. virginicus L.			
var. _australis_ (Scribn. & Ball) Hitchc.			
var. _submuticus_ Hook.			
var. _glabriflorus_ (Vasey) Bush			
var. _intermedius_ (Vasey) Bush			
Hystrix patula Moench			
Hordeum jubatum L.	B. (4), (2)	C. Hs	D. 10
H. pusillum Nutt.	B. (1)	C. Th	D. 10, 18
*_Lolium perenne_ L.	B. (4)	C. Hs	D. 10
*_L. multiflorum_ Lam.	B. (1)	C. Th	D. 10, 18
*_L. temulentum_ L.			
Sphenopholis obtusata (Michx.) Scribn.	B. (4)	C. Hs	D. 10
S. intermedia (Rydb.) Rydb.			
S. nitida (Spreng.) Scribn.			
Deschampsia flexuosa (L.) Trin.			
*_Arrhenatherum elatius_ (L.) Beauv.			
*_Holcus lanatus_ L.			
Danthonia spicata (L.) Beauv.			
D. compressa Austin			
D. sericea Nutt.			

Calamagrostis canadensis (Michx.) Beauv.			
C. cinnoides (Muhl.) Bart.			
**Agrostis alba* L.	B. (4)	C. Hsr	D. 10
A. palustris Huds.			
A. elliottiana Schultes	B. (1)	C. Th	D. 10, 18
A. hyemalis (Walt.) BSP.	B. (4)	C. Hs	D. 10
A. perennans (Walt.) Tuckerm.			
Cinna arundinacea L.			
**Alopecurus carolinianus* Walt.	B. (1)	C. Th	D. 10, 18
**Phleum pratense* L.	B. (4)	C. Hs	D. 10
Muhlenbergia cuspidata (Torr.) Rydb.			
M. sobolifera (Muhl.) Trin.	B. (4)	C. Hsr	D. 10
M. tenuiflora (Willd.) BSP.			
M. racemosa (Michx.) BSP.			
M. mexicana (L.) Trin.			
M. sylvatica Torr.			
M. schreberi Gmel.	B. (4)	C. Hs	D. 10
M. capillaris (Lam.) Trin.			
Sporobolus asper (Michx.) Kunth			
S. clandestinus (Spreng.) Hitchc.			
S. vaginiflorus (Torr.) Wood	B. (1)	C. Th	D. 10, 18
S. neglectus Nash			
S. poiretii (R. & S.) Hitchc.			
Brachyelytrum erectum (Schreb.) Beauv.	B. (4)	C. Hsr.	D. 10
Oryzopsis racemosa (J. E. Sm.) Ricker	B. (4)	C. Grh	D. 10
Stipa avenacea L.	B. (4)	C. Hs	D. 10
Aristida dichotoma Michx.	B. (1)	C. Th	D. 10, 18
A. oligantha Michx.			
A. ramossissima Engelm.			
A. longespica Poir.			
A. purpurascens Poir.	B. (4)	C. Hs	D. 10
A. affinis (Schult.) Kunth	B. (1)	C. Th	D. 10, 18
Leptochloa filiformis (Lam.) Beauv.			
**Eleusine indica* Gaertn.			
**Cynodon dactylon* (L.) Pers.	B. (4)	C. Hsr	D. 10
Spartina pectinata Link	B. (4)	C. Grh	D. 10
Gymnopogon ambiguus (Michx.) BSP.	B. (4)	C. Hsr	D. 10
Bouteloua curtipendula (Michx.) Torr.			
**Anthoxanthum odoratum* L.	B. (4)	C. Hs	D. 10
**Phalaris canariensis* L.	B. (4)	C. Grh	D. 10
P. arundinacea L.			
Leersia lenticularis Michx.	B. (4)	C. Hsr	D. 10
L. oryzoides (L.) Sw.			
L. virginica Willd.			
Zizania aquatica L.	B. (1)	C. Th	D. 10, 18
Zizaniopsis miliacea (Michx.) Döll & Aschers.	B. (4)	C. Grh	D. 10
**Digitaria sanguinalis* (L.) Scop.	B. (1)	C. Th	D. 10, 18
D. ischaemum (Schreb.) Muhl.			

D. violascens Link			
D. filiformis (L.) Koel.			
Paspalum fluitans (Ell.) Kunth	B. (4)	C. Hs	D. 10
P. repens Berg.			
P. pubiflorum Rupr.			
var. *glabrum* Vasey			
P. floridanum Michx.			
var. *glabratum* Engelm.			
P. longepedunculatum LeConte			
P. setaceum Michx.			
P. pubescens Muhl.			
P. laeve Michx.			
P. circulare Nash			
Panicum depauperatum Muhl.			
P. linearifolium Scribn.			
P. werneri Scribn.			
P. xalapense HBK.			
P. microcarpon Muhl.			
P. dichotomum L.			
P. meridionale Ashe			
P. barbulatum Michx.			
P. yadkinense Ashe			
P. lindheimeri Nash			
P. huachucae Ashe			
var. *fasciculatum* (Torr.) F. T. Hubb.			
P. tennesseense Ashe			
P. villosissimum Nash			
P. sphaerocarpon Ell.			
P. polyanthes Schultes			
P. ravenelii Scribn. & Merr.			
P. scoparium Lam.			
P. ashei Pearson			
P. commutatum Schultes			
P. clandestinum L.			
P. latifolium L.			
P. boscii Poir. var. *molle* (Vasey) Hitchc. & Chase			
P. dichotomiflorum Michx.	B. (1)	C. Th	D. 10, 18
P. flexile (Gattinger) Scribn.			
P. gattingeri Nash			
P. philadelphicum Bernh.			
P. capillare L.			
var. *occidentale* Rydb.			
P. virgatum L.	B. (4)	C. Grh	D. 10
P. agrostoides Spreng.	B. (4)	C. Hs	D. 10
P. stipitatum Nash			
P. longifolium Torr.			
P. anceps Michx.	B. (4)	C. Grh	D. 10
P. verrucosum Muhl.	B. (1)	C. Th	D. 10, 18
Echinochloa crusgalli (L.) Beauv.			
var. *mitis* (Pursh) Peterm.			
E. walteri (Pursh) Heller			
**Setaria lutescens* (Weigel) F. T. Hubb.			

**S. verticellata* (L.) Beauv.			
**S. viridis* (L.) Beauv.			
**S. italica* (L.) Beauv.			
Cenchrus pauciflorus Benth.			
**Miscanthus sinensis* Anderss.	B. (4)	C. Hs	D. 10
Erianthus alopecuroides (L.) Ell.			
E. giganteus (Walt.) Muhl.			
**Eulalia viminea* (Trin.) Kuntze	B. (1)	C. Th	D. 10, 18
Andropogon scoparius Michx.	B. (4)	C. Hs	D. 10
A. divergens (Hack.) Anderss.			
A. furcatus Muhl.			
A. ternarius Michx.			
A. virginicus L.			
A. glomeratus (Walt.) BSP.			
A. elliottii Chapm.			
**Sorghum halapense* (L.) Pers.	B. (4)	C. Grh	D. 10
**S. vulgare* Pers.	B. (1)	C. Th	D. 10, 18
Sorghastrum nutans (L.) Nash	B. (4)	C. Grh	D. 10
Tripsacum dactyloides L.			

8. *Cyperaceae*

A. Genera: 11. Species: 125. B. (4)—115. (1)—10.
C. H—78. Th—10. G.—33 (+1). HH—2 (+1).
D. 10—118. 11—7. 17—33. 18—10.

Dulichium arundinaceum (L.) Britt.	B. (4)	C. HH	D. 10
Cyperus flavescens L. var. *poaeformis* (Pursh) Fern.	B. (1)	C. Th	D. 10, 18
C. diandrus Torr.			
C. rivularis Kunth			
C. inflexus Muhl.			
C. esculentus L.	B. (4)	C. Gst	D. 10, 17
C. erythrorhizos Muhl.	B. (1)	C. Th	D. 10, 18
C. strigosus L.	B. (4)	C. Gst	D. 10, 17
C. refractus Engelm.			
C. retrofractus (L.) Torr.			
C. dipsaciformis Fern.			
C. hystricinus Fern.			
C. cylindricus (Ell.) Britt.			
C. ovularis (Michx.) Torr.			
Kyllinga pumila Michx.	B. (1)	C. Th	D. 10, 18
Scirpus americanus Pers.	B. (4)	C. HH	D. 10
S. validus Vahl	B. (4)	C. HH	D. 11
S. atrovirens Muhl. var. *georgianus* Harper	B. (4)	C. Hsr	D. 10
S. polyphyllus Vahl			
S. lineatus Michx.			
S. cyperinus (L.) Kunth			
Eleocharis acicularis (L.) R. & S.	B. (4)	C. Grh	D. 11, 17
E. obtusa (Willd.) Schultes	B. (1)	C. Th	D. 11, 18
E. engelmanni Steud.			
E. calva Torr.	B. (4)	C. Grh	D. 11, 17
E. tenuis (Willd.) Schultes var. *verrucosa* Svenson			
E. compressa Sulliv.			
Fimbristylis autumnalis (L.) R. & S. var. *mucronulata* (Michx.) Fern.	B. (1)	C. Th	D. 10, 18

Bulbostylis capillaris (L.) C. B. Clarke var. *crebra* Fern.			
Rynchospora glomerata (L.) Vahl	B. (4)	C. Hpr	D. 10
R. corniculata (Lam.) Gray	B. (4)	C. Hp	D. 10
Scleria triglomerata Michx.	B. (4)	C. Grh	D. 10, 17
S. oligantha Michx.			
S. ciliata Michx.			
S. pauciflora Muhl.			
Carex retroflexa Muhl.	B. (4)	C. Hs	D. 10
C. texensis (Torr.) L. H. Bailey	B. (4)	C. Hsr	D. 10
C. rosea Schkuhr	B. (4)	C. Hs	D. 10
C. convoluta Mack.			
C. radiata (Wahl.) Dew.			
C. cephalophora Muhl.			
C. leavenworthii Dew.	B. (4)	C. Grh	D. 10, 17
C. mesochorea Mack.			
C. muhlenbergii Schkuhr			
C. plana Mack.			
C. gravida Bailey			
C. aggregata Mack.			
C. sparganioides Muhl.			
C. annectens Bickn.	B. (4)	C. Hs	D. 10
C. vulpinoidea Michx.	B. (4)	C. Grh	D. 10, 17
C. stipata Muhl.	B. (4)	C. Hs	D. 10
C. uberior (C. Mohr) Mack.			
C. laevivaginata (Kükenth.) Mack.			
C. crus-corvi Shuttlw.			
C. conjuncta Boott			
C. incomperta Bickn.			
C. bromoides Schkuhr			
C. muskingumensis Schwein.			
C. scoparia Schkuhr			
C. projecta Mack.			
C. normalis Mack.			
C. festucacea Schkuhr			
C. brevior (Dew.) Mack.			
C. albolutescens Schwein.			
C. tribuloides Wahlenb.			
C. cristatella Britton			
C. leptalea Wahlenb.	B. (4)	C. Hsr	D. 10
C. jamesii Schwein.	B. (4)	C. Hs	D. 10
C. artitecta Mack.			
C. emmonsii Dew.			
C. communis Bailey			
C. pennsylvanica Lam.	B. (4)	C. Grh	D. 10, 17
C. umbellata Schkuhr	B. (4)	C. Hsr	D. 10
C. hirtifolia Mack.	B. (4)	C. Grh	D. 10, 17
C. eburnea Boott			
C. meadii Dew.			
C. plantaginea Lam.	B. (4)	C. Hs	D. 10
C. careyana Torr.			
C. platyphylla Carey			
C. digitalis Willd.			
C. purpurifera Mack.			

C. laxiflora Lam.
  var. *serrulata* Hermann
C. striatula Michx.
C. leptonervia Fern.
C. albursina Sheld.
C. blanda Dew.
C. gracilescens Steud.
C. granularis Muhl.
  var. *recta* Dew.
C. oligocarpa Schkuhr
C. hitchcockiana Dew.
C. amphibola Steud.
  var. *turgida* Fern.
C. glaucodea Tuckerm.
C. gracillima Schw. B. (4) C. Grh D. 10, 17
C. prasina Wahlenb. B. (4) C. Hs D. 10
C. davisii Schwein & Torr. B. (4) C. Grh D. 10, 17
C. aestivalis M. A. Curtis B. (4) C. Hs D. 10
C. debilis Michx.
  var. *rudgei* Bailey
C. allegheniensis Mack.
C. swanii (Fern.) Mack.
C. virescens Muhl.
C. hirsutella Mack. B. (4) C. Grh D. 10, 17
C. caroliniana Schwein.
C. scabrata Schwein. B. (4) C. Hsr D. 10
C. shortiana Dew. B. (4) C. Hs D. 10
C. deamii Hermann
C. buxbaumii Wahlenb. B. (4) C. Hsr D. 10
C. torta Boott B. (4) C. Hs D. 10
C. gynandra Schwein. B. (4) C. Hsr D. 10
C. crinita Lam.
C. stricta Lam.
C. hystricina Muhl.
C. comosa Boott B. (4) C. Hs D. 10
C. frankii Kunth B. (4) C. Hsr. D. 10
C. squarrosa L. B. (4) C. Hs D. 10
C. typhina Michx.
C. lurida Wahlenb.
C. baileyi Britton
C. grayii Carey
C. intumescens Rudge
C. louisianica L. H. Bailey B. (4) C. Grh, HH
  D. 10, 17
C. lupulina Muhl. B. (4) C. Hsr D. 10
C. lupuliformis Sartwell
C. gigantea Rudge
C. willdenowii Schk.
  (Harlan County — Anderson,
  1947. IA)
Cymophyllus fraseri (Andr.) Mack.

9. *Araceae*

A. Genera: 4. Species: 6. B. (4)—6. C. G—3. HH—3. D. 16—3. 17—3.
Acorus calamus L. B. (4) C. HH D.16
Orontium aquaticum L.

Arisaema dracontium (L.) Schott B. (4) C. Gst D. 17
A. triphyllum (L.) Schott
A. atrorubens (Ait.) Blume
Peltandra virginica (L.) Kunth B. (4) C. HH D. 16

10. *Lemnaceae*

A. Genera: 3. Species: 3. B. (4)—3. C. HH—3. D. 19—3.
Spirodela polyrhiza (L.) Schleid. B. (4) C. HH D. 19
Lemna minor L.
Wolffia punctata Griseb.

11. *Xyridaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. H—1. D. 14—1.
Xyris torta J. E. Smith B. (4) C. Hr D. 14

12. *Commelinaceae*

A. Genera: 2. Species: 7. B. (4)—5. (1)—2. C. H—4. Grh—1. Th—2. D. 16—4. 17—1. 18—2.
Commelina communis L. B. (1) C. Th D. 18
C. diffusa Burm. f.
C. elegans HBK. B. (4) C. Hp D. 16
C. virginica L. B. (4) C. Grh D. 17
Tradescantia canaliculata Raf. B. (4) C. Hp D. 16
T. subaspera Ker
T. virginiana L.

13. *Pontederiaceae*

A. Genera: 2. Species: 3. B. (4)—3. C. HH—3. D. 16—2. 19—1.
Heteranthera limosa (Sw.) Willd. B. (4) C. HH D. 19
H. reniformis R. & P. B. (4) C. HH D. 16
Pontederia cordata L.

14. *Juncaceae*

A. Genera: 2. Species: 17. B. (4)—16. (1)—1. C. H—11. G—5. Th—1. D. 10—15. 11—2. 18—1.
Juncus bufonius L. B. (1) C. Th D. 11, 18
J. effusus L.
var. *solutus* Fern. & Wieg. B. (4) C. Hr D. 11
J. macer S. F. Gray B. (4) C. Hr D. 10
J. coriaceus Mack. B. (4) C. Hs D. 10
J. marginatus Rostk.
J. biflorus Ell. B. (4) C. Grh D. 10
J. torreyi Cov. B. (4) C. Gst D. 10
J. canadensis J. Gay B. (4) C. Grh D. 10
J. subcaudatus (Engelm.) Cov. & Blake
J. diffusissimus Buckl. B. (4) C. Hs D. 10
J. brachycarpus Engelm. B. (4) C. Grh D. 10
J. acuminatus Michx. B. (4) C. Hs D. 10
J. debilis A. Gray
Luzula carolinae S. Wats. B. (4) C. Hsr D. 10
L. multiflora (Ehrh.) Lejeune B. (4) C. Hs D. 10
L. multiflora X *echinata* var. *mesochorea*
L. echinata (Small) Herm. var. *mesochorea* Herm.

15. *Liliaceae*

A. Genera: 22. Species: 51. B. Sh—5. (4)—46. C. M—5. Ch—1. H—2. G—43. D. 3—1. 5—5. 7—5. 9—1. 15—2. 17—37.
Chamaelirium lutem (L.) Gray B. (4) C. Grh D. 17

Stenanthium gramineum (Ker) Kunth	B. (4)	C. Gb	D. 17
S. robustum Wats.			
Veratrum parviflorum Michx.	B. (4)	C. Grh	D. 17
V. woodii Robbins			
Uvularia grandiflora J. E. Sm.			
U. perfoliata L.			
U. sessilifolia L.			
**Hemerocallis fulva* L.			
Allium tricoccum Ait.	B. (4)	C. Gb	D. 17
**A. vineale* L.			
A. canadense L.			
A. cernuum Roth			
Nothoscordum bivalve (L.) Britt.			
Lilium philadelphicum L.			
L. superbum L.			
L. canadense L.			
L. michiganense Farw.			
Erythronium albidum Nutt.			
E. americanum Ker			
Camassia scilloides (Raf.) Cory			
**Ornithogalum umbellatum* L.			
Yucca filamentosa L.	B. (4)	C. Ch	D. 9
**Asparagus officinalis* L.	B. (4)	C. Grh	D. 17
Clintonia umbellulata (Michx.) Morong			
Smilacina racemosa (L.) Desf. var. *cylindrata* Fern.			
Disporum maculatum (Buckl.) Britt.			
D. lanuginosum (Michx.) Nichols			
Streptopus roseus Michx. var. *perspectus* Fassett			
Polygonatum biflorum (Walt.) Ell.			
P. pubescens (Willd.) Pursh			
P. canaliculatum (Muhl.) Pursh			
Medeola virginiana L.			
Trillium sessile L.			
T. hugeri Small			
T. luteum (Muhl.) Harbison			
T. recurvatum Beck			
T. erectum L.			
T. gleasoni Fern.			
T. grandiflorum (Michx.) Salisb.			
T. nivale Riddell			
T. undulatum Willd.			
Aletris farinosa L.			
Smilax pulverulenta Michx.	B. (4)	C. Hpr	D. 15
S. herbacea L. var. *lasioneura* (Hock) A.DC.			
S. ecirrhata (Engelm.) Wats.	B. (4)	C. Grh	D. 17
S. glauca Walt.	B. Sh	C. M	D. 5, 7
S. bona-nox L.			
S. rotundifolia L. var. *quadrangulata* (Muhl.) Wood			
S. hispida Muhl.			
S. laurifolia L.	B. Sh	C. M	D. 3, 5, 7

16. *Amaryllidaceae*

A. Genera: 3. Species: 3. B. (4)—3. C. G—3. D. 17—3.

Hymenocallis occidentalis (LeConte) Kunth B. (4) C. Gb D. 17
Agave virginica L.
Hypoxis hirsuta (L.) Cov. var. *leptocarpa* (Engelm. & Gray) Brackett B. (4) C. Gst D. 17

17. *Dioscoreaceae*

A. Genera: 1. Species: 4. B. (4)—4. C. G—4. D. 15—4, 17—4.

Dioscorea villosa L. B. (4) C. Grh D. 15, 17
D. hirticaulis Bartlett
D. glauca Muhl.
D. quaternata (Walt.) Gmel.

18. *Iridaceae*

A. Genera: 3. Species: 7. B. (4)—7. C. H—3. G—4. D. 16—3. 17—4.

Iris verna L. B. (4) C. Grh D. 17
I. cristata Ait.
I. virginica L. var. *shrevei* (Small) E. Anders.
**Belamcanda chinensis* (L.) DC.
Sisyrinchium albidum Raf. B. (4) C. Hsr D. 16
S. angustifolium Mill
S. graminoides Bickn.

19. *Orchidaceae*

A. Genera: 16. Species: 32. B. (4)—32. C. H—9. G—23. D. 14—4. 16—5. 17—19. 20—4.

Cypripedium calceolus L. var. *pubescens* (Willd.) Correll B. (4) C. Grh D. 17
C. acaule Ait.
Orchis spectabilis L. B. (4) C. Grt D. 17
Habenaria flava (L.) Gray
H. clavellata (Michx.) Spreng.
H. cristata (Michx.) R. Br.
H. ciliaris (L.) R. Br.
H. blephariglottis (Willd.) Hook. var. *integrilabia* Correll
H. lacera (Michx.) R. Br.
H. psycodes (L.) Spreng.
H. peramoena Gray
Cleistes divaricata (L.) Ames B. (4) C. Gr D. 17
Triphora trianthophora (Sw.) Rydb. B. (4) C. Grt D. 17
Isotria verticillata (Willd.) Raf. B. (4) C. Gr D. 17
Spiranthes beckii Lindl. B. (4) C. Hr D. 14
S. gracilis (Bigel.) Beck
S. vernalis Engelm. & Gray B. (4) C. Hs D. 16
S. lucida (H. H. Eaton) Ames
S. ovalis Lindl.
S. cernua (L.) Richard
Listera smallii Wiegand
Goodyera pubescens (Willd.) R. Br. B. (4) C. Hrr D. 14
Calopogon pulchellus (Sw.) R. Br. B. (4) B. Gst D. 17
Corallorrhiza wisteriana Conrad B. (4) C. Grh D. 17, 20
C. odontorhiza (Willd.) Nutt.

C. maculata Raf.
C. striata Lindl.
Malaxis unifolia Michx. B. (4) C. Gst D. 17
Liparis liliifolia (L.) Richard B. (4) C. Hr D. 14
Tipularia discolor (Pursh) Nutt. B. (4) C. Gst D. 17
Hexalectris spicata (Walt.) Barnh. B. (4) C. Grh D. 17
Aplectrum hyemale (Muhl.) Torr. B. (4) C. Gst D. 17

Dicotyledonae

Families: 108. A. Genera: 484. Species: 1375.
B. T—134 (+6). Sh—168. (4)—756 (+7). (2)—86 (+10). (1)—231 (+16).
C. MM—107 (+3). M—122 (+4). N—56 (+2). Ch—25. H—724. G—98. HH—19. Th—232 (+5). S—1. E—1.
D. 1—1. 2—134 (+7). 3—12. 4—115 (+2). 5—44 (+1). 7—66. 9—7. 12—22. 14—70. 15—10. 16—630 (+2). 17—98. 18—232 (+2). 19—15. 20—15.

20. *Saururaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. HH—1. D. 16—1.
Saururus cernuus L. B. (4) C. HH D. 16

21. *Salicaceae*

A. Genera: 2. Species: 15. B. T—10 (+1). Sh—5. C. MM—8 (+1). M—5 (+2). N—2 (+2). D. 2—10 (+1). 4—5.
**Populus alba* L. B. T C. MM D. 2
P. heterophylla L.
P. candicans Ait
P. deltoides Marsh. B. T C. MM D. 2
P. grandidentata Michx.
Salix nigra Marsh.
**S. fragilis* L.
S. caroliniana Michx. B. T C. M (N) D. 2
**S. alba* L. B. T C. MM (M) D. 2
S. interior Rowlee B. T C. M D. 2
S. discolor Muhl. B. Sh (T) C. M (N) D. 4 (2)
S. sericea Marsh. B. Sh C. N D. 4
S. humilis Marsh.
var. *microphylla* (Anderss.) Fern.
S. rigida Muhl. B. Sh C. M D. 4
**S. purpurea* L.

22. *Myricaceae*

A. Genera: 1. Species: 1. B. Sh—1. C. N—1. D. 4—1
Comptonia peregrina (L.) Coult. B. Sh C. N D. 4

23. *Juglandaceae*

A. Genera: 2. Species: 10. B. T—10. C. MM—10. D. 2—10.
Juglans nigra L. B. T C. MM D. 2
J. cinerea L.
Carya illinoensis (Wang.) K. Koch
C. cordiformis (Wang.) K. Koch
C. ovata (Mill.) K. Koch
C. laciniosa (Michx. f.) Loud.
C. tomentosa (Lam.) Nutt.
C. glabra (Mill.) Sweet
C. ovalis (Wang.) Sarg.
var. *obovalis* Sarg.
var. *obcordata* (Muhl.) Sarg.
C. pallida (Ashe) Engl. & Graebn.

24. *Betulaceae*

A. Genera: 5. Species: 8. B. T—7 (+1). Sh—1 (+1). C. MM—6. M—2 (+2). D. 2—7 (+1). 4—1 (+1).

Carpinus caroliniana Walt.			
var. *virginiana* (Marsh.) Fern.	B. T	C. MM (M)	D. 2
Ostrya virginiana (Mill.) K. Koch			
Corylus americana Walt.	B. Sh, T	C. M	D. 4, 2
Betula nigra L.	B. T	C. MM	D. 2
B. lenta L.			
B. lutea Michx. f.			
var. *macrolepis* Fern.			
B. allegheniensis Britt.			
Alnus rugosa (DuRoi) Spreng.	B. T, Sh	C. M	D. 2, 4

25. *Fagaceae*

A. Genera: 3. Species: 21. B. T—21. C. MM—21. M—(1). D. 2—21.

Fagus grandifolia Ehrh.	B. T	C. MM	D. 2
Castanea dentata (Marsh.) Borkh.			
C. pumila (L.) Mill.			
Quercus alba L.			
Q. bicolor Willd.			
Q. muhlenbergii Engelm.			
Q. prinus L.			
Q. montana Willd.			
Q. stellata Wang.			
Q. macrocarpa Michx.			
Q. lyrata Walt.			
Q. phellos L.			
Q. imbricaria Michx.			
X. *Q. leana* Nutt.			
Q. rubra L.			
Q. velutina Lam.			
Q. palustris Muench.			
Q. shumardii Buckley			
var. *schneckii* Britt.			
Q. coccinea Muench.			
Q. falcata Michx.			
Q. marilandica Muench.	B. T	C. MM (M)	D. 2

26. *Ulmaceae*

A. Genera: 3. Species: 9. B. T—8. Sh—1 (+1). C MM—7. M—2. D. 2—8 (+1). 4—1.

Planera aquatica (Walt.) J. F. Gmel.	B. T	C. M	D. 2
Ulmus fulva Michx.	B. T	C. MM	D. 2
U. americana L.			
U. thomasi Sarg.			
U. alata Michx.			
U. serotina Sarg.			
Celtis occidentalis L.			
var. *crassifolia* (Lam.) Gray			
C. laevigata Willd.			
C. pumila (Muhl.) Pursh			
var. *deamii* Sarg.	B. Sh, T	C. M	D. 4, 2
var. *georgiana* (Small) Sarg.			

27. *Moraceae*

A. Genera: 5. Species: 6. B. T—4. (4)—1. (1)—1. C. MM—4. G—1. Th—1. D. 2—4. 15—1. 17—1. 18—1.

Morus rubra L.	B. T	C. MM	D. 2
M. alba L.			
var. *tatarica* (L.) Loud.			
**Broussonetia papyrifera* (L.) Vent.			
Maclura pomifera (Raf.) Schneid.			
Humulus americanus Nutt.	B. (4)	C. Grh	D. 15, 17
**Cannabis sativa* L.	B. (1)	C. Th	D. 18

28. *Urticaceae*

A. Genera: 5. Species: 7. B. (4)—3. (1)—4. C. G—2. H—1. Th—4. D. 16—1. 17—2. 18—4.

Urtica chamaedryoides Pursh	B. (1)	C. Th	D. 18
U. procera Muhl. in Willd.	B. (4)	C. Hpr	D. 16
Laportea canadensis (L.) Gaud.	B. (4)	C. Grh	D. 17
Pilea pumila (L.) Gray	B. (1)	C. Th	D. 18
Boehmeria cylindrica (L.) Sw.	B. (4)	C. Grh	D. 17
Parietaria pennsylvanica Muhl.	B. (1)	C. Th	D. 18
P. floridana Nutt.			

29. *Loranthaceae*

A. Genera: 1. Species: 1. B. Sh—1. C. E—1. D. 3—1. 20—1.

Phoradendron flavescens (Pursh) Nutt.	B. Sh	C. E	D. 3, 20

30. *Santalaceae*

A. Genera: 2. Species: 3. B. Sh—1. (4)—2. C. N—1. Grh—2. D. 4—1. 17—2. 20—1.

Comandra richardsiana Fern.	B. (4)	C. Grh	D. 17
C. umbellata (L.) Nutt.			
Pyrularia pubera Michx.	B. Sh	C. N	D. 4, 20

31. *Aristolachiaceae*

A. Genera: 2. Species: 5. B. (4)—5. C. H—3. Grh—2. D. 14—3. 17—2.

Asarum canadense L.	B. (4)	C. Hrr	D. 14
var. *reflexum* (Bickn.) Robins.			
var. *acuminatum* Ashe			
A. virginicum L.			
A. arifolium Michx.			
Aristolochia serpentaria L.	B. (4)	C. Grh	D. 17
A. durior Hill			

32. *Polygonaceae*

A. Genera: 4. Species: 29. B. Sh—1. (4)—15. (1)—13. C. M—1. H—12. G—1. HH—2. Th—13. D. 5—1. 7—1. 16—14. 17—1. 18—13.

**Rumex acetosella* L.	B. (4)	C. Hsr	D. 16
R. altissimus Wood	B. (4)	C. Hs	D. 16
R. verticillatus L.			
R. triangulivalvis (Danser) Rech. f.			
**R. crispus* L.			
**R. obtusifolius* L.			
Polygonum exsertum Small	B. (1)	C. Th	D. 18
P. erectum L.			
P. buxiforme Small			
P. aviculare L.			
P. tenue Michx.			
P. muhlenbergii (Meisn.) Wats.	B. (4)	C. Hp	D. 16

P. natans A. Eaton	B. (4)	C. HH	D. 16
P. pennsylvanicum L. var. *laevigatum* Fern.	B. (1)	C. Th	D. 18
P. lapathifolium L.			
P. hydropiper L. var. *projectum* Stanford			
P. punctatum Ell.	B. (4)	C. Hp	D. 16
**P. persicaria* L.	B. (1)	C. Th	D. 18
P. hydropiperoides Michx.	B. (4)	C. Hp	D. 16
P. setaceum Baldw. var. *tonsum* Fern.	B. (4)	C. HH	D. 16
**P. orientale* L.	B. (1)	C. Th	D. 18
P. virginianum L.	B. (4)	C. Grh	D. 17
P. sagittatum L.	B. (1)	C. Th	D. 7, 18
**P. convolvulus* L.	B. (1)	C. Th	D. 18
P. dumetorum L.	B. (4)	C. Hp	D. 16
P. scandens L.			
**P. cuspidatum* Sieb & Zucc.			
**Fagopyrum esculentum* Moench.	B. (1)	C. Th	D. 18
Brunnichia cirrhosa Gaertn.	B. Sh	C. M	D. 5

33. *Chenopodiaceae*

A. Genera: 3. Species: 8. B. (4)—1. (1)—7. C. H—1. Th—7. D. 16—1. 18—7.

**Chenopodium ambrosioides* L. ssp. *eu-ambrosioides* Aellen	B. (4)	C. Hp	D. 16
**C. botrys* L.	B. (1)	C. Th	D. 18
C. album L.			
C. hybridum L. var. *gigantospermum* (Aellen) Rouleau			
**C. murale* L.			
C. Standleyanum Aellen			
Atriplex patula L.			
Salsola pestifer A. Nels.			

34. *Amaranthaceae*

A. Genera: 4. Species: 10. B. (4)—1. (1)—9. C. H—1. Th—9. D. 16—1. 18—9.

**Celosia argentea* L.	B. (1)	C. Th	D. 18
**Amaranthus cruentus* L.			
**A. hybridus* L.			
**A. retroflexus* L.			
**A. spinosus* L.			
A. blitoides Wats.			
A. graecizans L.			
Acnida tamariscina (Nutt.) Wood			
A. altissima Riddell var. *subnuda* (Wats.) Fern.			
Iresine rhizomatosa Standl.	B. (4)	C. Hp	D. 16

35. *Nyctaginaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. G—1. D. 17—1.

Oxybaphus nyctagineus (Michx.) Sweet	B. (4)	C. Grt	D. 17

36. *Phytolaccaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. G—1. D. 17—1.

Phytolacca americana L.	B. (4)	C. Grt	D. 17

37. *Aizoaceae*

A. Genera: 1. Species: 1. B. (1)—1. C. Th—1. D. 18—1.

**Mollugo verticillata* L.	B. (1)	C. Th	D. 18

38. *Portulacaceae*

A. Genera: 2. Species: 3. B. (4)—2. (1)—1. C. G—2. Th—1. D. 17—2. 18—1.

Claytonia virginica L.	B. (4)	C. Gst	D. 17
C. caroliniana Michx.			
**Portulaca oleracea* L.	B. (1)	C. Th	D. 18

39. *Caryophyllaceae*

A. Genera: 11. Species: 31. B. (4)—13 (+1). (2)—2. (1)—16. C. Ch—5 (+1). H—10. Th—16. D. 12—5. 16—10. 18—16.

Stellaria longifolia Muhl.	B. (4)	C. Ch	D. 12
S. pubera Michx. var. *silvatica* (Beguinot) Weath.	B. (4)	C. Ch, Hp	D. 12, 16
**S. media* (L.) Cyrill.	B. (1)	C. Th	D. 18
**S. graminea* L. (Harlan County — Barbour and Barbour, 1950. CU)			
S. fontinalis (Short & Peter) Robins.	B. (4)	C. Ch	D. 12
**Cerastium vulgatum* L. var. *hirsutum* Fries	B. (4), (2)	C. Ch	D. 12
C. arvense L.	B. (4)	C. Ch	D. 12
**C. viscosum* L.	B. (1)	C. Th	D. 18
**C. nutans* Raf.			
**Holosteum umbellatum* L.	B. (2)	C. Hp	D. 16
**Arenaria serpyllifolia* L.	B. (1)	C. Th	D. 18
A. patula Michx.			
**Spergula arvensis* L.			
Paronychia canadensis (L.) Wood			
P. fastigiata (Raf.) Fern. var. *paleacea* Fern.			
**Agrostemma githago* L.			
Silene stellata (L.) Ait. var. *scabrella* (Nieuwland) Palm. & Steyerm.	B. (4)	C. Hs	D. 16
S. ovata Pursh			
**S. cucubalus* Wibel	B. (4)	C. Hpr	D. 16
**S. dichotoma* Ehrh.	B. (1)	C. Th	D. 18
S. antirrhina L.			
**S. noctiflora* L.			
S. caroliniana Walt. var. *wherryi* (Small) Fern.	B. (4)	C. Hs	D. 16
S. regia Sims	B. (4)	C. Hp	D. 16
S. virginica L.	B. (4)	C. Hs	D. 16
S. rotundifolia Nutt.			
**Lychnis alba* Mill.	B. (2)	C. Hs	D. 16
**Dianthus armeria* L.	B. (1)	C. Th	D. 18
**D. prolifer* L.			
**Saponaria officinalis* L.	B. (4)	C. Hpr	D. 16
**S. vaccaria* L.	B. (1)	C. Th	D. 18

40. *Nymphaceae*

A. Genera: 5. Species: 5. B. (4)—5. C. HH—5. D. 19—5.

Nelumbo lutea (Willd.) Pers.	B. (4)	C. HH	D. 19

Cabomba caroliniana Gray
Brasenia schreberi Gmel.
Nymphaea tuberosa Paine
Nuphar advena Ait.

41. *Ceratophyllaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. HH—1. D. 19—1.

Ceratophyllum demersum L.	B. (4)	C. HH	D. 19

42. *Ranunculaceae*

A. Genera: 15. Species: 44. B.—Sh—6. (4)—35. (1)—3. C. M—5. N—1. H—25. G—10. Th—3. D. 4—1. 5—5. 14—2. 16—23. 17—10. 18—3.

Hydrastis canadensis L.	B. (4)	C. Grh	D. 17
Isopyrum biternatum (Raf.) T. & G.	B. (4)	C. Hsr	D. 16
Xanthorhiza simplicissima Marsh.	B. Sh	C. N	D. 4
Actaea pachypoda Ell.	B. (4)	C. Grh	D. 17
Cimicifuga americana Michx.			
C. racemosa (L.) Nutt.			
Aquilegia canadensis L.	B. (4)	C. Hs	D. 16
**Delphinium ajacis* L.	B. (1)	C. Th	D. 18
D. tricorne Michx.	B. (4)	C. Hs	D. 16
Aconitum uncinatum L.	B. (4)	C. Hsr	D. 16
Anemone quinquefolia L. var. *interior* Fern.	B. (4)	C. Grh	D. 17
A. caroliniana Walt.	B. (4)	C. Gst	D. 17
A. canadensis L.	B. (4)	C. Hs	D. 16
A. lancifolia Pursh			
A. virginiana L.			
Anemonella thalictroides (L.) Spach	B. (4)	C. Grt	D. 17
Hepatica acutiloba DC.	B. (4)	C. Hr	D. 14
H. americana (DC.) Ker			
Clematis viorna L.	B. Sh	C. M	D. 5
C. pitcheri T. & G.			
C. ridgwayi Standl.			
C. versicolor Small			
C. virginiana L.			
Trautvetteria carolinensis (Walt.) Vail	B. (4)	C. Grh	D. 17
Ranunculus repens L.	B. (4)	C. Hsr	D. 16
**R. acris* L. (Harlan County — Barbour and Barbour, 1950. CU)	B. (4)	C. Grh	D. 17
**R. bulbosus* L.	B. (4)	C. Hs	D. 16
R. recurvatus Poir.			
R. carolinianus DC.			
R. septentrionalis Poir.	B. (4)	C. Hsr	D. 16
R. hispidus Michx.	B. (4)	C. Hs	D. 16
R. fascicularis Muhl.			
R. abortivus L.			
***R. allegheniensis* Britt. (*Gibson 265*, Adair County — F.)			
R. micranthus Nutt. var. *delitescens* (Greene) Fern.			
R. pusillus Poir.	B. (1)	C. Th	D. 18

R. sceleratus L.
Thalictrum clavatum DC. B. (4) C. Hs D. 16
T. coriaceum (Britt.) Small B. (4) C. Grh D. 17
T. dioicum L. B. (4) C. Hs D. 16
T. revolutum DC.
T. polygamum Muhl.
(Harlan County — Barbour and Barbour. 1950. CU)
T. dasycarpum Fisch. & Lall.
T. perelegans Greene

43. *Berberidaceae*

A. Genera: 4. Species: 4. B. Sh—1. (4)—3. C. M—1. G—3. D. 4—1. 7—1. 17—3.
Podophyllum peltatum L. B. (4) C. Grh D. 17
Jeffersonia diphylla (L.) Pers.
Caulophyllum thalictroides (L.) Michx.
***Berberis thunbergii* DC.
(*Gibson 164,* Adair County — F.) B. Sh C. M D. 4, 7

44. *Menispermaceae*

A. Genera: 3. Species: 3. B. Sh—3. C. M—3. D. 5—3. 9—1.
Menispermum canadense L. B. Sh C. M D. 5, 9
Cocculus carolinus (L.) DC. B. Sh C. M D. 5
Calycocarpum lyoni (Pursh) Nutt.

45. *Magnoliaceae*

A. Genera 2. Species: 5. B. T—5. C. MM—3. M—2. D. 2—5.
Magnolia acuminata L. B. T C. M D. 2
M. macrophylla Michx. B. T C. MM D. 2
M. tripetala L. B. T C. M D. 2
M. fraseri Walt. B. T C. MM D. 2
Liriodendron tulipifera L.

46. *Calycanthaceae*

A. Genera: 1. Species: 1. B. Sh—1. C. M—1. D. 2—1.
Calycanthus fertilis Walt. B. Sh C. M D. 2

47. *Anonaceae*

A. Genera: 1. Species: 1. B. T—1. C. M—1. D. 2—1.
Asimina triloba (L.) Dunal B. T C. M D. 2

48. *Lauraceae*

A. Genera: 2. Species: 2. B. T—1. Sh—1. C. MM—1. M—1. D. 2—1. 4—1.
Sassafras albidum (Nutt.) Nees
var. *molle* (Raf.) Fern. B. T C. MM D. 2
Lindera benzoin (L.) Blume
var. *pubescens* Palm. & Steyerm. B. Sh C. M D. 4

49. *Papaveraceae*

A. Genera: 3. Species: 3. B. (4)—2. (2)—1. C. G—1. H—2. D. 16—2. 17—1.
Sanguinaria canadensis L. B. (4) C. Grh D. 17
Stylophorum diphyllum (Michx.) Nutt. B. (4) C. Hs D. 16
**Chelidonium majus* L. B. (2) C. Hs D. 16

50. *Fumariaceae*

A. Genera: 3. Species: 5. B. (4)—2. (2)—3. C. G—2. H—3. D. 15—1. 16—2. 17—2.

Dicentra canadensis (Goldie) Walp.	B. (4)	C. Grt	D. 17
D. cucullaria (L.) Bernh.	B. (4)	C. Gb	D. 17
Adlumia fungosa (Ait.) Greene	B. (2)	C. Hs	D. 15
Corydalis sempervirens (L.) Pers.	B. (2)	C. Hs	D. 16
C. flavula (Raf.) DC.			

51. *Cruciferae*

A. Genera: 22. Species: 56. B. (4)—22 (+2). (2)—18 (+6). (1)—16. C. G—10. H—27. Th—17. HH—2. D. 16—27. 17—10. 18—17. 19—2.

**Lepidium campestre* (L.) R. Br.	B. (2)	C. Hs	D. 16
L. virginicum L.	B. (2), (1)	C. Hs	D. 16
**L. densiflorum* Schrad.			
**Thlaspi arvense* L.	B. (1)	C. Th	D. 18
**T. perfoliata* L.			
**Alliaria officinalis* Andrz.	B. (2)	C. Hp	D. 16
**Sisymbrium officinale* (L.) Scop. var. *leiocarpum* DC.	B. (1)	C. Th	D. 18
**S. altissimum* L.	B. (2)	C. Hs	D. 16
**S. thalianum* (L.) J. Gay	B. (1)	C. Th	D. 18
**Brassica campestris* L.	B. (2), (1)	C. Hs	D. 16
**B. juncea* (L.) Coss.	B. (1)	C. Th	D. 18
**B. kaber* (DC.) L. C. Wheeler var. *pinnatifida* (Stokes) L. C. Wheeler			
**B. nigra* (L.) Koch			
**Barbarea vulgaris* R. Br	B. (4)	C. Hs	D. 16
**B. verna* (Mill.) Asch.	B. (4), (2)	C. Hs	D. 16
Iodanthus pinnatifidus (Michx.) Steud.	B. (4)	C. Hs	D. 16
Rorippa sessiliflora (Nutt.) Hitchc.	B. (2), (1)	C. Hs	D. 16
R. islandica (Oeder ex Murr.) Borbás var. *microcarpa* (Regel) Fern.			
R. sylvestris (L.) Bess.	B. (4)	C. Hs	D. 16
**Nasturtium officinale* R. Br.	B. (4)	C. HH	D. 19
Lesquerella globosa (Desv.) Wats.	B. (2)	C. Hs	D. 16
Armoracea aquatica (Eaton) Wieg.	B. (4)	C. HH	D. 19
Cardamine bulbosa (Schreb.) BSP.	B. (4)	C. Gst	D. 17
C. douglassii (Torr.) Britt.			
C. rotundifolia Michx.	B. (4)	C. Hsr	D. 16
C. pennsylvanica Muhl.	B. (2)	C. Hs	D. 16
C. parviflora L. var. *arenicola* (Britt.) O. E. Schulz			
C. hirsuta (L.) Scop.	B. (1)	C. Th	D. 18
C. flexuosa With.	B. (2)	C. Hs	D. 16
Dentaria laciniata Muhl.	B. (4)	C. Gst	D. 17
D. multifida Muhl.	B. (4)	C. Grh	D. 17
D. multifida X *heterophylla*			
D. diphylla Michx.			
D. maxima Nutt.			
D. incisa Small	B. (4)	C. Gst	D. 17
D. anomola Eames			

D. heterophylla Nutt.
Leavenworthia uniflora
(Michx.) Britt. B. (1) C. Th D. 18
**Capsella bursa-pastoris* (L.) Medic.
**Camelina sativa* (L.) Crantz
**C. microcarpa* Andrz.
Draba brachycarpa Nutt.
D. cuneifolia Nutt.
**D. verna* L.
D. ramosissima Desv.
var. *glabrifolia* Braun B. (4) C. Hsr D. 16
Descurainia pinnata (Walt.) Britt.
var. *brachycarpa* (Richards.) Fern. B. (2) C. Hs D. 16
Arabis virginica (L.) Poir.
A. glabra (L.) Bernh.
A. lyrata L. B. (4), (2) C. Hs D. 16
A. laevigata (Muhl.) Poir.
var. *Burkii* Porter B. (2) C. Hs D. 16
A. perstellata Braun
var. *shortii* Fern. B. (4) C. Hs D. 16
A. perstellata X *A. laevigata*
A. canadensis L. B. (2) C. Hs D. 16
**Erysimum repandum* L. B. (1) C. Th D. 18
**Alyssum alyssoides* L.
**Hesperis matronalis* L. B. (2), (4) C. Hs D. 16

52. *Podostemaceae*

A. Genera: 1. Species: 1. B (4)—1. C. HH—1. D. 19—1.
Podostemum ceratophyllum Michx. B. (4) C. HH D. 19

53. *Crassulaceae*

A. Genera: 2. Species: 3. B. (4)—2 (+1). (2)—1. C. Ch—2. H—1. D. 12—2. 16—1.
Sedum pulchellum (L.) Scop. B. (2), (4) C. Ch D. 12
S. ternatum Michx. B. (4) C. Ch D. 12
Penthorum sedoides L. B. (4) C. Hpr D. 16

54. *Saxifragaceae*

A. Genera: 12. Species: 21. B. Sh—6. (4)—15. C. N—6. H—15. D. 4—4. 5—2. 7—2. 9—3. 14—12. 16—3.
Astilbe biternata (Vent.) Britt. B. (4) C. Hp D. 16
Boykinia aconitifolia Nutt. B. (4) C. Hrr D. 14
Sullivantia ohionis T. & G. B. (4) C. Hr D. 14
Saxifraga virginiensis Michx. B. (4) C. Hrr D. 14
S. micranthidifolia (Haw.) Britt. B. (4) C. Hr D. 14
S. leucanthemifolia Michx.
Tiarella cordifolia L. B. (4) C. Hrr D. 14
Heuchera villosa Michx.
var. *macrorhiza* (Small) R., B. & L. B. (4) C. Hr D. 14
var. *intermedia* R., B. & L.
H. parviflora Bartl.
var. *rugelii* (Shuttlw.) R., B. & L.
H. puberula Mack. & Bush
H. americana L.
var. *interior* R., B. & L.
var. *brevipetala* R., B. & L.
H. pubescens Pursh
var. *brachyandra* R., B. & L.

H. longiflora Rydb. B. (4) C. Hrr D. 14
Mitella diphylla L. B. (4) C. Hsr D. 16
Parnassia asarifolia Vent. B. (4) C. Hs D. 16
Philadelphus hirsutus Nutt. B. Sh C. N D. 4, 9
P. inodorus L.
Hydrangea arborescens L.
var. *Deamii* St. John
Itea virginica L. B. Sh C. N D. 4
Ribes cynosbati L. B. Sh C. N D. 5, 7
R. missouriensis (Nutt.) Cov. & Britt.

55. *Hamamelidaceae*

A. Genera: 2. Species: 2. B. T—1. Sh—1. C. MM—1. M—1. D. 2—1. 4—1.

Hamamelis virginica L. B. Sh C. M D. 4
Liquidambar styraciflua L. B. T C. MM D. 2

56. *Platanaceae*

A. Genera: 1. Species: 1. B. T—1. C. MM—1. D. 2—1.

Platanus occidentalis L. B. T C. MM D. 2

57. *Rosaceae*

A. Genera: 18. Species: 82. B. T—28. Sh—36. (4)—17. (2)—1. C. MM—2. M—39. N—9. H—32. D. 2—28. 4—24. 5—12. 7—43. 14—2. 16—16.

Physocarpus opulifolius (L.) Maxim. B. Sh C. N D. 4
**Spiraea japonica* L.
S. tomentosa L.
var. *rosea* (Raf.) Fern.
Aruncus dioicus (Walt.) Fern.
var. *pubescens* (Rydb.) Fern. B. (4) C. Hp D. 16
Gillenia stipulata (Muhl.) Trel.
G. trifoliata (L.) Moench.
Malus coronaria (L.) Mill. B. T C. M D. 2
M. lancifolia Rehd.
Aronia melanocarpa (Michx.) Ell. B. Sh C. N D. 4
A. prunifolia (Marsh.) Rehder
Amelanchier intermedia Spach B. T C. M D. 2
A. canadensis (L.) Medic.
***A. arborea* (Michx. f.) Fern.
(*Gibson & Watson 321*,
Adair County — F)
A. laevis Wiegand.
Crataegus crus-galli L. B. T C. M D. 2, 7
C. armata Beadle
C. wilkinsonii Ashe
C. engelmannii Sarg. B. T C. M D. 2
C. punctata Jacq. B. T C. M D. 2, 7
C. collina Chapm.
C. viridis L.
C. pratensis Sarg.
C. neobushii Sarg. B. Sh C. M D. 4, 7
C. rubella Beadle
C. boyntonii Beadle B. T C. M D. 2, 7
C. buckleyi Beadle
C. straminea Beadle B. Sh C. M D. 4, 7
C. macrosperma Ashe
C. iracunda Beadle B. T C. M D. 2, 7

C. populnea Ashe			
C. pruinosa (Wendl.) K. Koch	B. Sh	C. M	D. 4, 7
C. rugosa Ashe			
C. mollis (T. & G.) Scheele	B. T	C. MM	D. 2, 7
C. coccinioides Ashe	B. T	C. M	D. 2, 7
C. cibaria Beadle	B. Sh	C. M	D. 4, 7
C. cibilis Ashe	B. T	C. M	D. 2, 7
C. uniflora Moench	B. Sh	C. M	D. 4, 7
C. phaenopyrum (L.f.) Medic.	B. T	C. M	D. 2, 7
C. calpodendron (Ehrh.) Medic.	B. Sh	C. M	D. 4, 7
C. pubifolia Ashe			
Rubus odoratus L.	B. Sh	C. Hp	D. 4
R. occidentalis L.	B. Sh	C. Hpr	D. 5, 7
**R. phoenicolasius* Maxim.	B. Sh	C. Hp	D. 5, 7
R. hispidus L.	B. Sh	C. Hpr	D. 5, 7
R. centralis Bailey			
R. flagellaris Willd.			
var. *invisus* Bailey			
R. baileyanus Britt.			
R. enslenii Tratt.			
R. trivialis Michx.			
R. argutus Link	B. Sh	C. Hp	D. 4, 7
R. frondosus Bigel.	B. Sh	C. Hp	D. 5, 7
R. allegheniensis Porter	B. Sh	C. Hp	D. 4, 7
R. canadensis L.	B. Sh	C. Hpr	D. 5, 7
R. ostryifolius Rydb.	B. Sh	C. Hp	D. 4, 7
Fragaria virginiana Duchesne			
var. *illinoensis* (Prince) Gray	B. (4)	C. Hrr	D. 14
**Duchesnea indica* (Andr.) Focke	B. (4)	C. Hsr	D. 16
**Potentilla recta* L.	B. (4)	C. Hs	D. 16
P. monspeliensis L.	B. (2)	C. Hs	D. 16
P. canadensis L.			
var. *villosissima* Fern.	B. (4)	C. Hsr	D. 16
P. simplex Michx.			
var. *argyrisma* Fern.			
Waldsteinia fragarioides (Michx.) Tratt.			
var. *parviflora* (Small) Fern.	B. (4)	C. Hrr	D. 14
Geum vernum (Raf.) T. & G.	B. (4)	C. Hs	D. 16
G. canadense Jacq.			
var. *grimesii* Fern. & Weath.			
G. virginianum L.			
Agrimonia gryposepala Wallr.	B. (4)	C. Hpr	D. 16
A. rostellata Wallr.			
A. pubescens Wallr.	B. (4)	C. Hp	D. 16
A. parviflora Ait.	B. (4)	C. Hpr	D. 16
**Sanguisorba minor* Scop.	B. (4)	C. Hs	D. 16
Rosa setigera Michx.			
var. *tomentosa* T. & G.	B. Sh	C. M	D. 5, 7
**R. rubiginosa* L.	B. Sh	C. N	D. 5, 7
**R. micrantha* Sm.	B. Sh	C. N	D. 4, 7
R. palustris Marsh.			
R. carolina L.			
var. *villosa* (Best) Rehder			
var. *glandulosa* (Crepin) Rehder			

Prunus americana Marsh.	B. T	C. M	D. 2
P. lanata (Sudw.) Mack. & Bush			
P. angustifolia Marsh. var. *varians* Wight & Hedrick	B. Sh	C. M	D. 4
P. hortulana Bailey	B. T	C. M	D. 2
P. munsoniana Wight & Hedrick			
P. virginiana L.	B. Sh	C. M	D. 4
P. serotina Ehrh.	B. T	C. MM	D. 2
**P. mahaleb* L.	B. T	C. M	D. 2

58. *Leguminosae*

A. Genera: 30. Species: 87. B. T—6 (+1). Sh—5. (4)—56. (2)—5. (1)—15 (+3). C. MM—5. M—3 (+1). N—3. Ch—1. H—56. G—4. Th—15. D. 2—6 (+1). 4—5. 5—1. 7—4. 12—1. 14—3. 15—2. 16—52. 17—4. 18—14.

Schrankia microphylla (Dryand) Britt.	B. (4)	C. Hp	D. 7, 16
Desmanthus illinoensis (Michx.) MacM.	B. (4)	C. Hp	D. 16
Cercis canadensis L.	B. T	C. M	D. 2
Cassia nictitans L. var. *leiocarpa* Fern.	B. (1)	C. Th	D. 18
C. fasciculata Michx. var. *robusta* (Pollard) Macbr.			
C. hebecarpa Fern. var. *longipila* Braun	B. (4)	C. Hp	D. 16
C. marilandica L.			
C. tora L.	B. (1)	C. Th	D. 18
Gleditsia triacanthos L.	B. T	C. MM	D. 2, 7
G. aquatica Marsh.			
Gymnocladus dioica (L.) Koch	B. T	C. MM	D. 2
Cladrastis lutea (Michx. f.) Koch			
Baptisia tinctoria (L.) R. Br. var. *crebra* Fern.	B. (4)	C. Hp	D. 16
B. leucophaea Nutt.			
B. leucantha T. & G.			
B. australis (L.) R. Br.			
**Medicago sativa* L.			
**M. lupulina* L.	B. (1)	C. Th	D. 18
**M. alba* Desr.	B. (2)	C. Hs	D. 16
**M. officinalis* (L.) Lam.			
**Trifolium arvense* L.	B. (1)	C. Th	D. 18
**T. pratense* L.	B. (4)	C. Hr	D. 14
**T. resupinatum* L.	B. (1)	C. Th	D. 18
**T. repens* L.	B. (4)	C. Hsr	D. 16
**T. hybridum* L.	B. (4)	C. Hr	D. 14
**T. reflexum* L. var. *glabrum* Lojac	B. (2), (1)	C. Hr	D. 14
**T. agrarium* L.	B. (1)	C. Th	D. 18
**T. procumbens* L.			
**T. dubium* Sibth.			
Psoralea onobrychis Nutt.	B. (4)	C. Hpr	D. 16
P. psoralioides (Walt.) Carey var. *eglandulosa* (Ell.) F. L. Freeman	B. (4)	C. Hp	D. 16
Amorpha fruticosa L.	B. Sh	C. M	D. 4

Petalostemum candidum (Willd.) Michx.	B. (4) C. Hp D. 16
P. purpureum (Vent.) Rydb.	
Tephrosia spicata (Walt.) T. & G.	
T. virginiana (L.) Pers.	
Wisteria macrostachya Nutt.	B. Sh C. M D. 5
Sesbania exaltata (Raf.) Cory	B. (1) C. Th D. 18
Robinia pseudo-acacia L.	B. T C. MM D. 2, 7
R. hispida L.	B. Sh, T C. N, M D. 4, 2
R. boyntonii Ashe	B. Sh C. N D. 4
R. kelseyi Cowell	
Astragalus distortus T. & G.	B. (4) C. Hp D. 16
A. canadensis L.	
**Coronilla varia* L.	B. (4) C. Gr D. 17
Stylosanthes biflora (L.) BSP. var. *hispidissima* (Michx.) Pollard & Ball	B. (4) C. Hp D. 16
S. riparia Kearney	
Desmodium pauciflorum (Nutt.) DC.	
D. acuminatum (Michx.) DC.	
D. nudiflorum (L.) DC.	
D. rotundifolium (Michx.) DC.	
D. canescens (L.) DC.	
D. illinoensis Gray	
D. bracteosum (Michx.) DC.	
D. laevigatum (Nutt.) DC.	
D. viridiflorum (L.) Beck	
D. dillenii Darl.	
D. paniculatum (L.) DC. var. *pubens* T. & G.	
D. sessilifolium (Torr.) T. & G.	
D. rigidum (Ell.) DC.	
D. ciliare DC.	
D. marilandicum (L.) DC.	
Lespedeza procumbens Michx.	
L. repens (L.) Bart.	
L. violacea (L.) Pers.	
L. nuttalii Darl.	
L. virginica (L.) Britt.	
L. intermedia (Wats.) Britt.	
L. simulata Mack. & Bush	
L. hirta (L.) Hornem.	
L. capitata Michx.	
**L. cuneata* G. Don	B. (1) C. Th D. 18
**L. stipulacea* Maxim.	
**L. striata* (Thunb.) H. & A.	
**Vicia angustifolia* Reichard	B. (2), (1) C. Hp D. 16
V. caroliniana Walt.	B. (4) C. Hp D. 16
**V. villosa* Roth	B. (2), (1) C. Hp D. 16
Lathyrus palustris L. var. *myrtifolius* (Muhl.) Gray	B. (4) C. Hp D. 15
Clitoria mariana L.	
Amphicarpa bracteata (L.) Fern. var. *comosa* (L.) Fern.	B. (4) C. Hpr D. 16

Apios americana Medic. B. (4) C. Gst D. 17
A. priceana Robins.
Galactia volubilis (L.) Britt.
var *mississippiensis* Vail B. (4) C. Hp D. 16
Phaseolus polystachyus (L.) BSP. B. (4) C. Ch D. 12
Strophostyles helvola (L.) Britt. B. (1) C. Th D. 18
S. umbellata (Muhl.) Britt. B. (4) C. Gr D. 17
S. leiosperma (T. & G.) Piper B. (1) C. Th D. 18

59. *Geraniaceae*

A. Genera: 1. Species: 4. B. (4)—1. (1)—3. C. H—1. Th—3. D. 16—1. 18—3.

Geranium maculatum L. B. (4) C. Hsr D. 16
G. carolinianum L. B. (1) C. Th D. 18
**G. columbinum* L.
**G. pusillum* Burm. f.

60. *Oxalidaceae*

A. Genera: 1. Species: 8. B. (4)—7. (2)—1. C. H—7. G—1. D. 16—7. 17—1.

Oxalis montana Raf. B. (4) C. Hrr D. 16
O. violacea L. B. (4) C. Gb D. 17
var. *trichophora* Fassett
O. grandis Small B. (4) C. Hpr D. 16
O. repens Thunb. B. (2) C. Hpr D. 16
O. stricta L. B. (4) C. Hp D. 16
var. *piletocarpa* Wieg.
O. florida Salisb.
O. europea Jord. B. (4) C. Hpr D. 16
var *Bushii* Small
O. recurva Ell.
var. *macrantha* (Trel.) Wieg.

61. *Linaceae*

A. Genera: 1. Species: 4. B. (4)—3. (1)—1. C. H—3. Th—1. D. 16—3. 18—1.

Linum sulcatum Riddell B. (1) C. Th D. 18
L. striatum Walt. B. (4) C. Hp D. 16
L. virginianum L.
L. medium (Planch.) Trel.
var. *texanum* (Planch.) Fern.

62. *Rutaceae*

A. Genera: 2. Species: 2. B. T—1 (+1). Sh—1 (+1). C. M—2. D. 2—2 (+1) 4—1 (+1). 7—1.

Zanthoxylum americanum Mill. B. T (Sh) C. M D. 2, 4, 7
Ptelea trifoliata L. B. Sh (T) C. M D. 4, 2

63. *Simarubaceae*

A. Genera: 1. Species: 1. B. T—1. C. MM—1. D. 2—1.

**Ailanthus altissima* (Mill.) Swingle B. T C. MM D. 2

64. *Polygalaceae*

A. Genera: 1. Species: 10. B. (4)—3. (1)—7. C. H—3. Th—7. D. 16—3. 18—7.

Polygala paucifolia Willd. B. (4) C. Hpr D. 16
P. polygama Walt. B. (4) C. Hp D. 16
P. senega L.
var. *latifolia* T. & G.

P. incarnata L.	B. (1)	C. Th	D. 18
P. ambigua Nutt.			
P. cruciata L.			
P. sanguinea L.			
P. nuttallii T. & G.			
P. curtisii Gray			
P. verticillata L.			
var. *ambigua* (Nutt.) Wood			
var. *isocycla* Fern.			

65. *Euphorbiaceae*

A. Genera: 6. Species: 22. B. (4)—4. (2)—2. (1)—16 (+2). C. H—5. G—1. Th—16. D. 16—17. 17—1. 18—4.

Phyllanthus caroliniensis Walt.	B. (1)	C. Th	D. 18
Croton glandulosus L.			
var. *septentrionalis* Muell. Arg.			
C. capitatus Michx.			
C. monanthogynus Michx.			
Crotonopsis elliptica Willd.			
Acalypha ostryaefolia Riddell			
A. rhomboidea Raf.			
A. virginica L.			
A. gracilens Gray			
Tragia cordata Michx.	B. (4)	C. Hp	D. 16
Euphorbia obtusata Pursh	B. (1)	C. Th	D. 18
E. chamaesyce L.			
E. maculata L.			
E. supina Raf.			
E. humistrata Engelm.			
E. marginata Pursh			
E. ipecacuanhae L.	B. (4)	C. Hp	D. 16
E. mercurialina Michx.			
E. corollata L.	B. (4)	C. Grt	D. 17
E. dentata Michx.	B. (1)	C. Th	D. 18
E. heterophylla L.	B. (2), (1)	C. Hp	D. 16
E. commutata Engelm.	B. (2), (1)	C. Hpr	D. 16

66. *Callitrichaceae*

A. Genera: 1. Species: 3. B. (4)—2. (1)—1. C. HH—2. Th—1. D. 18—1. 19—2.

Callitriche deflexa A. Br.			
var. *austini* (Engelm.) Hegelm.	B. (1)	C. Th	D. 18
C. palustris L.	B. (4)	C. HH	D. 19
C. heterophylla Pursh			

67. *Buxaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. H—1. D. 12—1.

Pachysandra procumbens Michx.	B. (4)	C. Hpr	D. 12

68. *Limnanthaceae*

A. Genera: 1. Species: 1. B. (1). C. Th—1. D. 18—1.

Floerkea proserpinacoides Willd.	B. (1)	C. Th	D. 18

69. *Anacardiaceae*

A. Genera: 1. Species: 5. B. Sh—5. C. MM—1 (+1). M—3. N—1. D. 4—4. 5—1 (+1).

Rhus typhina L.	B. Sh	C. M	D. 4
R. glabra L.			
R. copallina L.			
var. *latifolia* Engler			

R. radicans L.	B. Sh	C. MM (N)	D. 5 (4)
R. aromatica Ait.			
var. *illinoensis* (Greene) Rehder	B. Sh	C. N	D. 4

70. *Aquifoliaceae*

A. Genera: 1. Species: 4. B. T—2. Sh—2. C. M—4. D. 1—1. 2—1. 4—2.

Ilex opaca Ait.	B. T	C. M	D. 1
I. decidua Walt.	B. Sh	C. M	D. 4
I. montana Gray	B. T	C. M	D. 2
I. verticillata (L.) Gray	B. Sh	C. M	D. 4
var. *padifolia* (Willd.) T. & G.			

71. *Celastraceae*

A. Genera: 3. Species: 6. B. Sh—6. C. MM—1. M—1. N—4. D. 3—1. 4—2. 5—3.

Euonymus atropurpureus Jacq.	B. Sh	C. M	D. 4
**E. europaeus* L.	B. Sh	C. N	D. 5
E. americanus L.	B. Sh	C. N	D. 4
E. obovatus Nutt.	B. Sh	C. N	D. 5
Celastrus scandens L.	B. Sh	C. MM	D. 5
Pachistima canbyi A. Gray	B. Sh	C. N	D. 3

72. *Staphyleaceae*

A. Genera: 1. Species: 1. B. Sh—1. C. M—1. D. 4—1.

Staphylea trifolia L.	B. Sh	C. M	D. 4

73. *Aceraceae*

A. Genera: 1. Species: 6. B. T—6. C. MM—4. M—2. D. 2—6.

Acer negundo L.	B. T	C. MM	D. 2
A. pennsylvanicum L.	B. T	C. M	D. 2
A. spicatum Lam.			
A. saccharum Marsh.	B. T	C. MM	D. 2
var. *nigrum* (Michx. f.) Britt.			
var. *rugelii* (Pax) Rehder			
A. saccharinum L.			
A. rubrum L.			
var. *trilobum* K. Koch			
var. *drummondii* (H. & A.) Sarg.			

74. *Hippocastanaceae*

A. Genera: 1. Species: 2. B. T—2. C. MM—2. D. 2—2.

Aesculus glabra Willd.	B. T	C. MM	D. 2
A. octandra Marsh.			

75. *Balsaminaceae*

A. Genera: 1. Species: 2. B. (1)—2. C. Th—2. D. 18—2.

Impatiens biflora Walt.	B. (1)	C. Th	D. 18
I. pallida Nutt.			

76. *Rhamnaceae*

A. Genera: 3. Species: 4. B. Sh—4. C. MM—1. M—2. N—1. D. 4—4. 5—1.

Berchemia scandens (Hill) K. Koch	B. Sh	C. MM	D. 4, 5
Rhamnus lanceolata Pursh	B. Sh	C. M	D. 4
R. caroliniana Walt.			
var. *mollis* Fern.			
Ceanothus americanus L.	B. Sh	C. N	D. 4
var. *intermedius* (Pursh) Trel.			

77. *Vitaceae*

A. Genera: 2. Species: 10. B. Sh—10. C. MM—10. D. 5—10.

Vitis labrusca L.	B. Sh	C. MM	D. 5
V. aestivalis Michx.			
V. argentifolia Muns.			
V. cinerea Engelm.			
V. palmata L.			
V. vulpina L.			
V. riparia Michx.			
V. baileyana Muns.			
V. rotundifolia Michx.			
Parthenocissus quinquefolia (L.) Planch.			

78. *Tiliaceae*

A. Genera: 1. Species: 4. B. T—4. C. MM—4. D. 2—4.

Tilia americana L.	B. T	C. MM	D. 2
T. neglecta Spach			
T. floridana (V. Engler) Small			
T. heterophylla Vent. var. *michauxii* (Nutt.) Sarg.			

79. *Malvaceae*

A. Genera: 6. Species: 11. B. (4)—4. (2)—2. (1)—5 (+1). C. H—6. Th—5. D. 16—6. 18—5 (+1).

**Abutilon theophrasti* Medic.	B. (1)	C. Th	D. 18
**Malva moschata* L.	B. (2), (1)	C. Hs	D. 16 (18)
**M. neglecta* Wallr.			
Malvastrum angustum A. Gray	B. (1)	C. Th	D. 18
**Anoda cristata* (L.) Schlecht.			
**Sida spinosa* L.			
Hibiscus militaris Cav.	B. (4)	C. Hp	D. 16
H. moscheutos L.			
H. palustris L.			
H. lasiocarpus Cav.			
**H. trionum* L.	B. (1)	C. Th	D. 18

80. *Theaceae*

A. Genera: 1. Species: 1. B. Sh—1. C. N—1. D. 4—1.

Stewartia ovata (Cav.) Weath. var. *grandiflora* Weath.	B. Sh	C. N	D. 4

81. *Hypericaceae*

A. Genera: 2. Species: 16. B. Sh—5. (4)—9. (1)—2 (+2). C. N—5. H—9. Th—2. D. 4—6. 16—9 (+2). 18—2.

Ascyrum stans Michx.	B. Sh	C. N	D. 4
A. hypericoides L.			
var. *multicaule* (Michx.) Fern.			
var. *oblongifolium* (Spach) Fern.			
**Hypericum perforatum* L.	B. (4)	C. Hp	D. 16
H. punctatum Lam.	B. (4)	C. Hpr	D. 16
var. *pseudomaculatum* (Bush) Fern.			
H. frondosum Michx.	B. Sh	C. N	D. 4
H. densiflorum Pursh			
H. prolificum L.			
H. dolabriforme Vent.	B. (4)	C. Hpr	D. 16
H. sphaerocarpum Michx. var. *turgidum* (Small) Svenson	B. (4)	C. Hp	D. 16

H. denticulatum Walt.
H. mutilum L. B. (4), (1) C. Hp D. 16, 18
H. canadense L. B. (4), (1) C. Hpr D. 16, 18
H. Drummondii (Grev. & Hook.) T. & G. B. (1) C. Th D. 18
H. gentianoides (L.) BSP.
H. tubulosum Walt.
var. *Walteri* (Gmel.) Lott B. (4) C. Hpr D. 16
***H. virginicum* L.
(*Gibson and Watson 376*, Adair County — F.)

82. *Cistaceae*

A. Genera: 1. Species: 4. B. (4)—4. C. H—4. D. 16—4.
Lechea villosa Ell. B. (4) C. Hp D. 16
L. minor L. B. (4) C. Hpr D. 16
L. tenuifolia Michx. B. (4) C. Hp D. 16
L. racemulosa Lam.

83. *Violaceae*

A. Genera: 2. Species: 43. B. (4)—43. C. H—43. D. 14—37. 16—6.
Hybanthus concolor (Forster) Spreng. B. (4) C. Hp D. 16
Viola pedata L. B. (4) C. Hr D. 14
var. *lineariloba* DC.
V. pedatifida G. Don
V. stoneana House
V. palmata L. B. (4) C. Hrr D. 14
V. egglestonii Brainerd B. (4) C. Hr D. 14
V. triloba Schwein.
var. *dilatata* (Ell.) Brainerd
V. emarginata LeConte
var. *acutiloba* Brainerd B. (4) C. Hrr D. 14
V. cucullata Ait.
V. affinis LeConte
V. papilionacea Pursh B. (4) C. Hr D. 14
V. sororia Willd.
V. hirsutula Brainerd
V. fimbriatula J. E. Sm.
V. sagittata Ait.
V. lanceolata L. B. (4) C. Hrr D. 14
V. blanda Willd.
V. primulifolia L.
V. rotundifolia Michx.
V. hastata Michx. B. (4) C. Hr D. 14
V. tripartita Ell.
V. pubescens Ait.
var. *peckii* House
V. eriocarpa Schwein.
V. canadensis L. B. (4) C. Hs D. 16
V. striata Ait.
V. conspersa Reichenb.
V. rostrata Pursh
V. walteri House B. (4) C. Hrr D. 14

V. kitaebeliana R. & S.
var. *rafinesquii* (Greene) Fern. B. (4) C. Hr D. 14
V. affinis X *palmata* Dowell
V. affinis X *triloba* Brainerd
V. emarginata X *papilionacea* House
V. hirsutula X *sororia* Dowell
V. hirsutula X *triloba* Brainerd
V. palmata X *sororia* House
V. palmata X *triloba* Brainerd
V. papilionacea X *sororia* Brainerd
V. papilionacea X *stoneana* Brainerd
V. papilionacea X *triloba* Brainerd
V. sagittata X *sororia* Brainerd
V. sororia X *triloba* Brainerd
V. stoneana X *triloba* Brainerd
V. rostrata X *striata* Brainerd B. (4) C. Hr D. 16

84. *Passifloraceae*

A. Genera: 1. Species: 2. B. (4)—2. C. H—2. D. 15—2.
Passiflora lutea L.
var. *glabriflora* Fern. B. (4) C. Hp D. 15
P. incarnata L.

85. *Cactaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. S—1. D. 7—1.
Opuntia compressa (Salisb.) Macbr. B. (4) C. S D. 7

86. *Thymelaeaceae*

A. Genera: 1. Species: 1. B. Sh—1. C. N—1. D. 4—1.
Dirca palustris L. B. Sh C. N D. 4

87. *Lythraceae*

A. Genera: 6. Species: 7. B. (4)—3. (1)—4. C. Ch—1. H—1. Th—4. HH—1. D. 9—1. 16—2. 18—4.
Ammannia coccinea Rottb. B. (1) C. Th D. 18
A. koehnei Britt.
Didiplis diandra (Nutt.) Wood B. (4) C. HH D. 16
Rotala ramosior (L.) Koehne B. (1) C. Th D. 18
var. *interior* Fern. & Grisc.
Lythrum alatum Pursh B. (4) C. Hpr D. 16
Cuphea petiolata (L.) Koehne B. (1) C. Th D. 18
Decodon verticillatus (L.) Ell. B. (4) C. Ch D. 9
var. *laevigatus* T. & G.

88. *Melastomaceae*

A. Genera: 1. Species: 2. B. (4)—2. C. G—2. D. 17—2.
Rhexia virginica L. B. (4) C. Gr D. 17
R. mariana L.
var. *leisperma* Fern. & Grisc. B. (4) C. Gr D. 17

89. *Onagraceae*

A. Genera: 6. Species: 22. B. (4—14. (2)—7. (1)—1. C. H—18. G—2. Th—1. HH—1. D. 16—19. 17—2. 18—1. 19—1.
Jussiaea decurrens (Walt.) DC. B. (4) C. Hp D. 16
J. repens L.
var. *glabrescens* Ktze. B. (4) C. HH D. 16, 19
(Meade County — Davies, 1955.
Univ. Louisville herbarium.)
J. diffusa Forsk. B. (4) C. Hpr D. 16

Ludvigia palustris (L.) Ell. var. *americana* (DC.) Fern. & Grisc.			
L. alternifolia L.	B. (4)	C. Hp	D. 16
L. glandulosa Walt.			
L. hirtella Raf.			
Epilobium coloratum Muhl.	B. (4)	C. Hs	D. 16
Oenothera canovirens Steele	B. (2)	C. Hs	D. 16
O. laevigata Bartlett			
O. nutans Atkinson & Bartlett			
O. pratincola Bartlett			
O. pycnocarpa Atkinson & Bartlett			
O. laciniata Hill	B. (1)	C. Th	D. 18
O. perennis (L.) Pennell	B. (4)	C. Hs	D. 16
O. tetragona (Roth.) Pennell			
var. *longistipata* (Pennell) Munz			
var. *fraseri* (Pursh) Munz			
var. *brevistipata* (Pennell) Munz			
O. speciosa Nutt.			
***O. triloba* Nutt. (*McFarland 96* — Second Century Coll., Fayette County — F.)	B. (2)	C. Hs	D. 16
Gaura biennis L.			
G. filipes Spach	B. (4)	C. Hs	D. 16
Circaea quadrisulcata (Maxim.) Franch. & Sav. var. *canadensis* (L.) Hara	B. (4)	C. Grh	D. 17
C. alpina L.			

90. *Haloragidaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. HH—1. D. 19—1.

Proserpinaca palustris L. var. *crebra* Fern. & Grisc.	B. (4)	C. HH	D. 19

91. *Araliaceae*

A. Genera: 2. Species: 5. B. Sh—1. (4)—4. C. M—1. H—2. G—2. D. 4—1. 7—1. 16—2. 17—2.

Aralia nudicaulis L.	B. (4)	C. Hpr	D. 16
A. racemosa L.			
A. spinosa L.	B. Sh	C. M	D. 4, 7
Panax quinquefolius L.	B. (4)	C. Grh	D. 17
P. trifolium L.			

92. *Umbelliferae*

A. Genera: 24. Species: 35. B. (4)—26. (2) 2 (+1). (1)—7. C. Ch—1. H—21. G—4. HH—2. Th—7. D. 12—1. 14—1. 16—22. 17—4. 18—7. 19—1.

Hydrocotyle americana L.	B. (4)	C. Hrr	D. 14
Sanicula gregaria Bickn.	B. (4)	C. Hs	D. 16
S. canadensis L.	B. (2)	C. Hs	D. 16
S. trifoliata Bickn.	B. (4), (2)	C. Hs	D. 16
Eryngium yuccaefolium Michx.	B. (4)	C. Grh	D. 17
E. prostratum Nutt.	B. (4)	C. Ch	D. 12
Chaerophyllm procumbens (L.) Crantz	B. (1)	C. Th	D. 18
var. *shortii* T. & G.			
C. tainturieri Hook.			

Osmorhiza claytoni (Michx.) Greene	B. (4)	C. Hs	D. 16
O. longistylis (Torr.) DC.			
var. *villicaulis* Fern.			
**Torilis japonicus* (Houtt.) DC.	B. (1)	C. Th	D. 18
Erigenia bulbosa (Michx.) Nutt.	B. (4)	C. Grt	D. 17
**Conium maculatum* L.	B. (4)	C. Hs	D. 16
**Bupleurum rotundifolium* L.	B. (1)	C. Th	D. 18
Zizia aurea (L.) Koch	B. (4)	C. Hs	D. 16
Z. aptera (Gray) Fern.			
Z. bebbii (Coult. & Rose) Britt.			
Cicuta maculata L.			
Cryptotaenia canadensis (L.) DC.			
Taenidia integerrima (L.) Drude	B. (4)	C. Hp	D. 16
Ptilimnium capillaceum (Michx.) Raf.	B. (1)	C. Th	D. 18
P. nuttallii (DC.) Britt.			
Perideridia americana			
(Nutt.) Reichenb.	B. (4)	C. Grt	D. 17
Sium suave Walt.	B. (4)	C. HH	D. 16
**Aethusa cynapium* L.	B. (1)	C. Th	D. 18
Ligusticum canadense (L.) Britt.	B. (4)	C. Hs	D. 16
Thaspium trifoliatum (L.) Gray			
var. *flavum* Blake			
T. barbinode (Michx.) Nutt.			
var. *angustifolium* Coult. & Rose			
T. pinnatifidum (Buckl.) Gray			
Angelica curtisii Buckl.			
A. villosa (Walt.) BSP.			
Oxypolis rigidior (L.) Raf.	B. (4)	C. HH	D. 16, 19
**Pastinaca sativa* L.	B. (2)	C. Hs	D. 16
Heracleum lanatum Michx.	B. (4)	C. Grt	D. 17
**Daucus carota* L.	B. (4)	C. Hs	D. 16

93. *Cornaceae*

A. Genera: 2. Species: 11. B. T—4. Sh—7 (+1). C. MM—3. M—7. N—1. D. 2—4. 4—7 (+1).

Nyssa aquatica L.	B. T	C. MM	D. 2
N. sylvatica Marsh.			
var. *caroliniana* (Poir.) Fern.			
Cornus florida L.			
C. alternifolia L. f.	B. T, Sh	C. M	D. 2, 4
C. amomum Mill.	B. Sh	C. M	D. 4
C. asperifolia Michx.			
C. obliqua Raf.			
C. stricta Lam.			
C. stolonifera Michx.			
C. drummondii Mey.			
C. racemosa Lam.	B. Sh	C. N	D. 4

94. *Ericaceae*

A. Genera: 12. Species: 31. B. T—1 (+2). Sh—25. (4)—5. C. MM—1. M—11. N—12. Ch—1. H—3. G—3. D. 2—1 (+2). 3—10. 4—15. 14—1. 16—1. 17—3. 20—3.

Clethra acuminata Michx.	B. Sh	C. M	D. 4
Chimaphila maculata (L.) Pursh	B. (4)	C. Hpr	D. 16
Pyrola rotundifolia L.			
var. *americana* (Sweet) Fern.	B. (4)	C. Hrr	D. 14

Monotropa uniflora L. B. (4) C. Gr D. 17, 20
M. hypopithys L.
var. *rubra* (Torr.) Farw.
M. odorata Ell.
Rhododendron maximum L. B. Sh, T C. M D. 3, 2
R. catawbiense Michx. B. Sh C. M D. 3
R. calendulaceum (Michx.) Torr.
R. cumberlandense Braun B. Sh C. N D. 3
R. nudiflorum (L.) Torr.
R. roseum (Loisel.) Rehd. B. Sh C. M D. 3
R. arborescens (Pursh) Torr. B. Sh, T C. M D. 3, 2
Kalmia latifolia L. B. Sh C. M D. 3
Lyonia ligustrina (L.) DC. B. Sh C. M D. 4
and integrating varieties
salicifolia (Wats.) DC.
capreaefolia (Wats.) DC.
foliosiflora (Michx.) Fern.
pubescens (Gray) Rehder.
Oxydendrum arboreum (L.) DC. B. T C. MM D. 2
Epigaea repens L. B. Sh C. Ch D. 3
Gaultheria procumbens L. B. Sh C. Hpr D. 3
Gaylussacia brachycera (Michx.) Gray B. Sh C. N D. 4
G. baccata (Wang.) C. Koch
Vaccinium arboreum Marsh. B. Sh C. M D. 4
V. corymbosum L. B. Sh C. N D. 4
V. stamineum L.
V. neglectum (Small) Fern.
V. vacillans Torr.
V. constablaei Gray B. Sh C. M D. 4
V. simulatum Small
V. pallidum Ait. B. Sh C. N D. 4
V. alto-montanum Ashe
V. missouriense Ashe
V. missouriense X *vacillans*

95. *Diapensiaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. G—1. D. 17—1.
Galax aphylla L. B. (4) C. Grh D. 17

96. *Primulaceae*

A. Genera: 4. Species: 10. B. (4)—9. (1)—1. C. Ch—1. H—8. Th—1. D. 12—1. 14—1. 16—7. 18—1.
Samolus parviflorus Raf. B. (4) C. Hs D. 16
**Lysimachia nummularia* L. B. (4) C. Ch D. 12
L. quadrifolia L. B. (4) C. Hpr D. 16
L. terrestris (L.) BSP.
L. ciliata L.
L. tonsa Wood
L. lanceolata Walt.
L. hybrida Michx. B. (4) C. Hp D. 16
**Anagallis arvensis* L. B. (1) C. Th D. 18
Dodecathon meadia L. B. (4) C. Hr D. 14

97. *Sapotaceae*

A. Genera: 1. Species: 1. B. T—(1). Sh—1. C. M—(1). N—1. D. 2—(1). 4—1. 7—1.
Bumelia lycioides (L.) Gaertn. f. B. Sh. T C. N, M D. 4, 7, 2

98. *Ebenaceae*

A. Genera: 1. Species: 1. B. T—1. C. MM—1. D. 2—1.

Diospyros virginiana L. B. T C. MM D. 2
**var. *platycarpa* Sarg.
(*Gibson 106,* Adair County — F)

99. *Styracaceae*

A. Genera: 2. Species: 2. B. T—1. Sh—1. C. M—2. D. 2—1. 4—1.

Halesia carolina L. B. T C. M D. 2
Styrax americana Lam. B. Sh C. M D. 4

100. *Oleaceae*

A. Genera: 3. Species: 7. B. T—6. Sh—1. C. MM—5. M—2. D. 2—6. 4—1.

Fraxinus americana L. B. T C. MM D. 2
F. tomentosa Michx. f.
F. biltmoreana Beadle
F. pennsylvanica Marsh.
var. *lanceolata* (Borkh.) Sarg.
F. quadrangulata Michx.
Chionanthus virginica L. B. T C. M D. 2
Forestiera ligustrina (Michx.) Poir. B. Sh C. M D. 4

101. *Loganiaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. H—1. D. 16—1.

Spigelia marilandica L. B. (4) C. Hp D. 16

102. *Gentianaceae*

A. Genera: 5. Species: 13. B. (4)—8 (+1). (2)—3. (1)—2. C. H—11. Th—2. D. 16—11. 18—2.

Sabatia angularis (L.) Pursh B. (2) C. Hs D. 16
S. stellaris Pursh B. (1) C. Th D. 18
S. campanulata (L.) Torr. B. (4) C. Hs D. 16
Bartonia paniculata (Michx.) Robins. B. (2) C. Hp D. 16
Obolaria virginica L. B. (4) C. Hp D. 16
Gentiana quinquefolia L. B. (1) C. Th D. 18
var. *occidentalis* (Gray) Hitchc.
G. puberula Michx. B. (4) C. Hp D. 16
***G. andrewsii* Griseb.
(*Gibson 186* and *331,*
Adair County — F)
G. saponaria L. B. (4) C. Hpr D. 16
G. decora Pollard B. (4) C. Hp D. 16
G. flavida A. Gray
G. villosa L.
Frasera carolinensis Walt. B. (2), (4) C. Hs D. 16

103. *Apocynaceae*

A. Genera: 4. Species: 6. B. Sh—1. (4)—5. C. M—1. Ch—1. H—4. D. 5—1. 12—1. 16—4.

Amsonia tabernaemontana Walt. B. (4) C. Hp D. 16
var. *salicifolia* (Pursh) Woodson
**Vinca minor* L. B. (4) C. Ch D. 12
Trachelospermum difforme (Walt.) Gray B. Sh C. M D. 5
Apocynum cannabinum L. B. (4) C. Hp D. 16
var. *glaberrimum* A. DC.
var. *pubescens* (Mitchell) A. DC.
A. androsaemifolium L.
A. medium Greene

104. *Asclepiadaceae*

A. Genera: 5. Species: 19. B. (4)—19. C. H—16. G—3. D. 15—1. 16—16. 17—3.

Acerates hirtella Pennell	B. (4)	C. Hp	D. 16
A. viridiflora Ell.			
Asclepias tuberosa L.			
A. purpurascens L.			
A. incarnata L.			
A. amplexicaulis J. E. Sm.			
A. syriaca L.	B. (4)	C. Gr	D. 17
A. intermedia Vail	B. (4)	C. Hp	D. 16
A. sullivantii Engelm.	B. (4)	C. Hs	D. 16
A. phytolaccoides Pursh	B. (4)	C. Hp	D. 16
A. variegata L.			
A. quadrifolia Jacq.			
A. perennis Walt.			
A. verticillata L.			
Asclepiodora viridis (Walt.) Gray	B. (4)	C. Grh	D. 17
Ampelamus albidus (Nutt.) Britt.	B. (4)	C. Gr	D. 15, 17
Gonolobus gonocarpos (Walt.) Perry	B. (4)	C. Hp	D. 15
G. obliquus (Jacq.) Schultes			
G. shortii Gray			

105. *Convolvulaceae*

A. Genera: 4. Species: 13. B. (4)—4. (1)—9. C. H—2. G—2. Th—9. D. 15—1. 16—1. 17—2. 18—9. 20—5.

Cuscuta pentagona Engelm.	B. (1)	C. Th	D. 18, 20
C. cephalanthi Engelm.			
C. gronovii Willd.			
C. compacta Juss.			
C. campestris Yuncker			
Convolvulus spithamaeus L.	B. (4)	C. Hp	D. 16
C. sepium L. var. *repens* (L.) Gray	B. (4)	C. Hp	D. 15
C. arvensis L.	B. (4)	C. Gr	D. 17
**Ipomoea hederacea* Jacq.	B. (1)	C. Th	D. 18
**I. purpurea* (L.) Roth			
I. pandurata (L.) G. F. W. Mey. var. *rubescens* Choisy	B. (4)	C. Grt	D. 17
I. lacunosa L.	B. (1)	C. Th	D. 18
**Quamoclit coccinea* (L.) Moench			

106. *Polemoniaceae*

A. Genera: 2. Species: 12. B. (4)—12. C. Ch—2. H—10. D. 9—2. 16—10.

Phlox subulata L. var. *australis* Wherry	B. (4)	C. Ch	D. 9
P. bifida Beck. var. *stellaria* (Gray) Wherry	B. (4)	C. Hpr	D. 16
P. divaricata L.	B. (4)	C. Ch	D. 9
P. pilosa L.	B. (4)	C. Hp	D. 16
P. amoena Sims	B. (4)	C. Hpr	D. 16
P. stolonifera Sims			
P. carolina L. var. *triflora* (Michx.) Wherry			
P. glaberrima L. var. *interior* Wherry	B. (4)	C. Hp	D. 16

var. *melampyrifolia* (Salisb.) Wherry
P. maculata L.
var. *odorata* (Sweet) Wherry
var. *pyramidalis* (Smith) Wherry
P. amplifolia Britt.
P. paniculata L.
var. *acuminata* (Pursh) Chapm.
Polemonium reptans L.
var. *villosum* Braun

107. *Hydrophyllaceae*

A. Genera: 2. Species: 6. B. (4)—3. (2)—2. (1)—1. C. H—4. G—1. Th—1. D. 16—4. 17—1. 18—1.

Hydrophyllum appendiculatum Michx.	B. (2)	C. Hs	D. 16
H. canadense L.	B. (4)	C. Grh	D. 17
H. macrophyllum Nutt.	B. (4)	C. Hs	D. 16
H. virginianum L.	B. (4)	C. Hsr	D. 16
Phacelia bipinnatifida Michx.	B. (2)	C. Hp	D. 16
P. purshii Buckl.	B. (1)	C. Th	D. 18

108. *Boraginaceae*

A. Genera: 9. Species: 17. B. (4)—9 (+1). (2)—5. (1)—3. C. H—14. Th—3. D. 16—14. 18—3.

**Heliotropium indicum* L.	B. (1)	C. Th	D. 18
H. tenellum (Nutt.) Torr.			
**Cynoglossum officinale* L.	B. (2)	C. Hs	D. 16
C. virginianum L.	B. (4)	C. Hs	D. 16
**Lappula echinata* Gilib.	B. (1)	C. Th	D. 18
Hackelia virginiana (L.) I. M. Johnston	B. (2)	C. Hs	D. 16
Myosotis verna Nutt.			
M. macrosperma Engelm.			
Mertensia virginica (L.) Link	B. (4)	C. Hs	D. 16
**Lithospermum arvense* L.	B. (2)	C. Hs	D. 16
L. latifolium Michx.	B. (4)	C. Hp	D. 16
**L. officinale* L.			
L. tuberosum Rugel	B. (4)	C. Hs	D. 16
L. canescens (Michx.) Lehm.	B. (4)	C. Hp	D. 16
***L. croceum* Fern. (*Gibson 289*, Adair County — F.)			
Onosmodium hispidissimum Mack.	B. (4)	C. Hs	D. 16
**Echium vulgare* L.	B. (4), (2)	C. Hs	D. 16

109. *Verbenaceae*

A. Genera: 2. Species: 7. B. (4)—7. C. H—7. D. 16—7.

Verbena canadensis (L.) Britt.	B. (4)	C. Hpr	D. 16
V. urticaefolia L.	B. (4)	C. Hp	D. 16
V. simplex Lehm.			
V. hastata L.			
V. stricta Vent.			
V. bracteata Lag. & Rodr.			
Lippia lanceolata Michx. var. *recognita* Fern. & Grisc.	B. (4)	C. Hpr	D. 16

110. *Labiatae*

A. Genera: 28. Species: 72. B. Sh—1. (4)—61. (2)—4. (1)—6 (+1). C. N—1. H—59. G—6. Th—6. D. 4—1. 16—59. 17—6. 18—6.

Teucrium canadense L. var. *virginicum* (L.) Eaton	B. (4)	C. Hpr	D. 16
T. occidentale Gray			
Isanthus brachiatus (L.) BSP.	B. (1)	C. Th	D. 18
Trichostema dichotomum L.			
Scutellaria nervosa Pursh	B. (4)	C. Hpr	D. 16
S. ambigua Nutt.	B. (4)	C. Gst	D. 17
S. leonardi Epl.			
S. parvula Michx. var. *australis* (Fassett) Epl.			
S. laterifolia L.	B. (4)	C. Hpr	D. 16
S. saxatilis Riddell			
S. ovata Hill ssp. *calcarea* Epl.			
ssp. *pseudovenosa* Epl.			
S. incana Spreng.	B. (4)	C. Hp	D. 16
S. punctata Leon			
S. serrata Andr.			
S. ovalifolia Pers.	B. (4)	C. Hpr	D. 16
ssp. *mollis* Epl.			
ssp. *hirsuta* (Short) Epl.			
S. integrifolia L.			
**Marrubium vulgare* L.	B. (4)	C. Hp	D. 16
Agastache nepetoides (L.) Ktze.	B. (4)	C. Hs	D. 16
A. scrophulariaefolia (Willd.) Ktze.			
Meehania cordata (Nutt.) Britt.	B. (4)	C. Hpr	D. 16
**Nepeta cataria* L.	B. (4)	C. Hp	D. 16
**Glecoma hederacea* L. var. *parviflora* (Benth.) House	B. (4)	C. Hpr	D. 16
**Prunella vulgaris* L. var. *lanceolata* (Bart.) Fern.	B. (4)	C. Hsr	D. 16
Physostegia denticulata (Ait.) Britt.	B. (4)	C. Hp	D. 16
P. virginiana (L.) Benth.			
P. speciosa (Sweet) Sweet			
Synandra hispidula (Michx.) Britt.	B. (2)	C. Hp	D. 16
**Lamium amplexicaule* L.	B. (2), (1)	C. Hp	D. 16
**L. purpureum* L.	B. (1)	C. Th	D. 18
**L. cordiaca* L.	B. (4)	C. Hp	D. 16
**L. marrubiastrum* L.	B. (2)	C. Hp	D. 16
**L. sibiricus* L.			
Stachys tenuifolia Willd.	B. (4)	C. Hpr	D. 16
S. nuttallii Shuttlw.	B. (4)	C. Gst	D. 17
S. palustris L. var. *homotricha* Fern.			
S. riddellii House	B. (4)	C. Hpr	D. 16
Salvia urticifolia L.	B. (4)	C. Hs	D. 16
S. lyrata L.			
S. azurea Lam. var. *grandiflora* Benth.			
**S. sylvestris* L.	B. (4)	C. Hsr	D. 16
Monarda didyma L.	B. (4)	C. Hpr	D. 16
M. bradburiana Beck			

M. clinipodia L.
M. fistulosa L.
var. *mollis* (L.) Benth.
Blephilia ciliata (L.) Raf.
B. hirsuta (Pursh) Benth.
Hedeoma pulegioides (L.) Pers. — B. (1) C. Th D. 18
**Melissa officinalis* L. — B. (4) C. Hpr D. 16
**Satureja nepeta* (L.) Scheele
S. glabella (Michx.) Briq. — B. (4) C. Hp D. 16
S. vulgaris (L.) Fritsch — B. (4) C. Hpr D. 16
Conradina verticillata Jennison — B. Sh C. N D. 4
Pycnanthemum flexuosum (Walt.) BSP. — B. (4) C. Hpr D. 16
P. virginianum (L.) Durand & Jackson
P. pilosum Nutt.
P. verticillatum (Michx.) Pers.
P. albescens T. & G.
P. incanum (L.) Michx.
P. pycnanthemoides (Leavenw.) Fern.
Cunila origanoides (L.) Britt. — B. (4) C. Hp D. 16
Lycopus rubellus Moench — B. (4) C. Hpr D. 16
L. americanus Muhl.
L. uniflorus Michx.
L. virginicus L.
**Mentha longifolia* (L.) Huds.
var. *mollissima* (Borkh.) Rouy
(Meade County — Davies, 1955. Univ. Louisville herbarium.)
**M. spicata* L.
**M. piperita* L.
**M. citrata* Ehrh.
**M. arvensis* L.
var. *canadensis* (L.) Briq.
Collinsonia canadensis L. — B. (4) C. Gst D. 17
**Perilla frutescens* (L.) Britt. — B. (1) C. Th D. 18
***Mosla dianthera* (Hamilton) Maxim.
(*Braun 4874*, McCreary County — F)

111. *Solanaceae*

A. Genera: 5. Species: 12. B. Sh—2. (4)—5. (1)—5. C. M—1. N—1. G—5. Th—5. D. 5—2. 7—2. 17—5. 18—5.

**Nicandra physalodes* (L.) Pers. — B. (1) C. Th D. 18
**Lycium halimifolium* Mill. — B. Sh C. M D. 5
Physalis subglabrata Mack. & Bush — B. (4) C. Grh D. 17
P. virginiana Mill.
P. pubescens L. — B. (1) C. Th D. 18
P. heterophylla Nees — B. (4) C. Grh D. 17
P. ambigua (Gray) Rydb.
Solanum carolinense L. — B. (4) C. Gr D. 7, 17
S. rostratum Dunal — B. (1) C. Th D. 7, 18
S. nigrum L. — B. (1) C. Th D. 18
S. dulcamara L. — B. Sh C. N D. 5

**Datura stramonium* L.	B. (1)	C. Th	D. 18

112. *Scrophulariaceae*

A. Genera: 23. Species: 55. B. (4)—32. (2)—6. (1)—17 (+2). C. Ch—5. H—32. G—1. Th—17. D. 12—5. 16—32. 17—1. 18—17. 20—1.

Hydranthelium rotundifolium (Michx.) Pennell	B. (4)	C. Ch	D. 12
Gratiola neglecta Torr.	B. (1)	C. Th	D. 18
G. lutea Raf. (Harlan County — Barbour and Barbour. 1950. CU)			
G. virginiana L.			
Tragiola pilosa (Michx.) Small & Pennell	B. (4)	C. Hs	D. 16
Leucospora multifida (Michx.) Nutt.	B. (1)	C. Th	D. 18
Mimulus ringens L.	B. (4)	C. Hpr	D. 16
M. alatus Ait.			
Lindernia dubia (L.) Pennell var. *major* (Pursh) Pennell	B. (1)	C. Th	D. 18
L. anagallidea (Michx.) Pennell			
**Verbascum blattaria* L.	B. (2)	C. Hs	D. 16
**V. thapsus* L.			
**V. phlomoides* L.			
Chelone glabra L. var. *elatior* Raf.	B. (4)	C. Hpr	D. 16
C. obliqua L. var. *speciosa* Pennell & Wherry			
Penstemon digitalis Nutt.	B. (4)	C. Hs	D. 16
P. alluviorum Pennell			
P. calycosus Small			
P. laevigatus Ait.			
P. canescens Britt.			
P. pallidus Small			
P. brevisepalus Pennell			
P. tenuiflorus Pennell			
P. hirsutus (L.) Willd.			
Scrophularia marilandica L.	B. (4)	C. Hp	D. 16
Collinsia verna Nutt.	B. (2)	C. Hp	D. 16
**Linaria vulgaris* Hill	B. (4)	C. Hpr	D. 16
**Kickxia elatine* (L.) Dumort.	B. (1)	C. Th	D. 18
Veronicastrum virginicum (L.) Farw.	B. (4)	C. Grh	D. 17
**Veronica serpyllifolia* L.	B. (4)	C. Hp	D. 16
V. peregrina L.	B. (1)	C. Th	D. 18
**V. arvensis* L.			
**V. officinalis* L.	B. (4)	C. Ch	D. 12
V. americana (Raf.) Schwein.			
V. glandifera Pennell			
V. comosa Richter			
**V. persica* Poir.	B. (1)	C. Ch	D. 18
Aureolaria virginica (L.) Pennell	B. (4)	C. Hp	D. 16
A. laevigata (Raf.) Raf.			
A. flava (L.) Farw. var. *macrantha* Pennell			
A. patula (Chapm.) Pennell			

A. pedicularis (L.) Raf.
var. *austromontana* Pennell B. (2), (1) C. Hp D. 16
A. pectinata (Nutt.) Pennell
var. *eurycarpa* Pennell B. (1) C. Th D. 18
Dasistoma macrophylla (Nutt.) Raf. B. (4) C. Hp D. 16
Gerardia purpurea L. B. (1) C. Th D. 18
G. tenuifolia Vahl
var. *macrophylla* Benth.
G. skinneriana Wood
G. decemloba Greene
G. gattingeri Small
Buchnera americana L. B. (4) C. Hpr D. 16
Schwalbea australis Pennell B. (4) C. Hp D. 16
Pedicularis lanceolata Michx. B. (4) C. Hs D. 16
P. canadensis L.
Castilleja coccinea (L.) Spreng. B. (2), (1) C. Hs D. 16, 20
Melampyrum lineare Lam.
var. *pectinatum* Pennell B. (1) C. Th D. 18

113. *Bignoniaceae*

A. Genera: 4. Species: 4. B. T—2. Sh—2. C. MM—4. D. 2—2. 5—2.
Bignonia capreolata L. B. Sh C. MM D. 5
Campsis radicans (L.) Seem.
Catalpa speciosa Warder B. T C. MM D. 2
**Paulownia tomentosa* (Thunb.) Steud.

114. *Martyniaceae*

A. Genera: 1. Species: 1. B. (1)—1. C. Th—1. D. 18—1.
Proboscidea louisianica (Mill.) Thell. B. (1) C. Th D. 18

115. *Orobanchaceae*

A. Genera: 3. Species: 4. B. (4)—4. C. G—4. D. 17—4. 20—4.
Conopholis americana (L.f.) Wallr. B. (4) C. Gp D. 17, 20
Orobanche ludoviciana Nutt.
O. uniflora L.
Epifagus virginiana (L.) Bart.

116. *Lentibulariaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. HH—1. D. 19—1.
Utricularia gibba L. B. (4) C. HH D. 19

117. *Acanthaceae*

A. Genera: 2. Species: 4. B. (4)—4. C. G—3. HH—1. D. 16—1. 17—4.
Ruellia caroliniensis (Walt.) Steud. B. (4) C. Grh D. 17
var. *parviflora* (Nees) Blake
R. strepens L.
R. pedunculata Torr.
Justicia americana (L.) Vahl B. (4) C. HH D. 16

118. *Phrymaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. H—1. D. 16—1.
Phryma leptostachya L. B. (4) C. Hp D. 16

119. *Plantaginaceae*

A. Genera: 1. Species: 5. B. (4)—2. (2)—1 (+1). (1)—2 (+1). C. H—3. Th—2 (+1). D. 14—3. 18—2 (+1).
Plantago rugellii Dcne.
var. *asperula* Farw. B. (4) C. Hr D. 14
**P. lanceolata* L.
var. *sphaerostachya* Mert. & Koch B. (4), (2) C. Hr D. 14

P. aristata Michx. B. (1) C. Th D. 18
P. virginica L. B. (2), (1) C. Hr, Th D. 14, 18
P. pusilla Nutt. B. (1) C. Th D. 18

120. *Rubiaceae*

A. Genera: 6. Species: 24. B. Sh—1. (4)—21. (1)—2. C. M—1. Ch—1. H—20. Th—2. D. 4—1. 12—1. 16—20. 18—2.

Houstonia caerulea L. B. (4) C. Hsr D. 16
H. serpyllifolia Michx.
H. purpurea L.
var. *pubescens* Britt. B. (4) C. Hs D. 16
H. longifolia Gaertn.
H. lanceolata (Poir.) Britt.
H. tenuifolia Nutt.
H. canadensis Willd.
H. nigricans (Lam.) Fern.
Cephalanthus occidentalis L.
var. *pubescens* Raf. B. Sh C. M D. 4
Mitchella repens L. B. (4) C. Ch D. 12
Diodia teres Walt.
var. *setifera* Fern. & Grisc. B. (1) C. Th D. 18
D. virginiana L. B. (4) C. Hp D. 16
Spermacoce glabra Michx.
Galium aparine L. B. (1) C. Th D. 18
G. pilosum Ait. B. (4) C. Hp D. 16
var. *puncticulosum* (Michx.) T. & G.
G. circaezans Michx.
var. *hypomalacum* Fern. B. (4) C. Hpr D. 16
G. lanceolatum Torr. B. (4) C. Hp D. 16
G. latifolium Michx.
G. obtusum Bigel.
G. tinctorium L. B. (4) C. Hpr D. 16
**G. pedemontanum* All. B. (4) C. Hp D. 16
G. concinnum T. & G.
G. triflorum Michx.
G. trifidum L.
ssp. *tinctorium* (L.) Fern.

121. *Caprifoliaceae*

A. Genera: 5. Species: 21. B. Sh—18. (4)—3. C. M—14. N—4. H—3. D. 4—18. 16—3.

Sambucus canadensis L. B. Sh C. M D. 4
S. pubens Michx.
Viburnum acerifolium L.
V. recognitum Fern.
V. dentatum L.
var. *deamii* (Rehder) Fern.
var. *pubescens* (Ait.) Pursh
V. molle Michx.
V. rafinesquianum Schultes B. Sh C. N D. 4
V. affine Bush
var. *hypomalacum* Blake
V. cassinoides L. B. Sh C. M D. 4
V. lentago L.
V. prunifolium L.

V. rufidulum Raf.
Triosteum perfoliatum L. B. (4) C. Hp D. 16
T. aurantiacum Bickn.
var. *glaucescens* Wieg.
T. angustifolium L.
Symphoricarpos orbiculatus Moench B. Sh C. N D. 4
**Lonicera japonica* Thunb. B. Sh C. M D. 4
L. dioica L.
L. glaucescens Rydb.
L. prolifera (Kirchner) Rehd.
L. sempervirens L.

122. *Valerianaceae*

A. Genera: 2. Species: 2. B. (4)—1. (1)—1. C. H—1. Th—1. D. 16—1. 18—1.
Valerianella intermedia Dyal B. (1) C. Th D. 18
Valeriana pauciflora Michx. B. (4) C. Hsr D. 16

123. *Dipsacaceae*

A. Genera: 1. Species: 1. B. (2)—1. C. H—1. D. 16—1.
**Dipsacus sylvestris* Huds. B. (2) C. Hs D. 16

124. *Cucurbitaceae*

A. Genera: 4. Species: 4. B. (4)—2. (1)—2. C. H—2. Th—2. D. 15—2. 18—2.
Melothria pendula L. B. (4) C. Hp D. 15
Cucurbita foetidissima HBK.
Echinocystis lobata (Michx.) T. & G. B. (1) C. Th D. 18
Sicyos angulatus L.

125. *Campanulaceae*

A. Genera: 2. Species: 3. B. (4)—1. (2)—1. (1)—1. C. H—2. Th—1. D. 16—2. 18—1.
Campanula americana L. B. (2) C. Hp D. 16
C. divaricata Michx. B. (4) C. Hpr D. 16
Specularia perfoliata (L.) A. DC. B. (1) C. Th D. 18

126. *Lobeliaceae*

A. Genera: 1. Species: 7. B. (4)—5. (2)—2. C. H—7. D. 16—7.
Lobelia cardinalis L. B. (4) C. Hs D. 16
L. siphilitica L.
L. amoena Michx.
L. puberula Michx.
L. nuttallii R. & S.
L. inflata L. B. (2) C. Hs D. 16
L. spicata Lam.
var. *originalis* McVaugh
var. *leptostachys* (A. DC.) Mack. & Bush

127. *Compositae*

A. Genera: 61. Species: 248. B. (4)—190 (+1). (2)—17 (+3). (1)—41 (+6). C. Ch—5. H—185. G—17. Th—41. D. 7—10. 12—5. 14—5. 16—181. 17—17. 18—41.
Vernonia noveboracensis (L.) Michx. B. (4) C. Hp D. 16
V. fasciculata Michx.
V. altissima Nutt.
V. missurica Raf.
Elephantopus carolinianus Willd.
E. tomentosus L.

Eupatorium maculatum L. (Harlan County — Barbour & Barbour, 1950. CU).			
E. fistulosum Barrett			
E. purpureum L.			
E. serotinum Michx.			
E. album L.			
var. *glandulosum* (Michx.) Fern.			
var. *monardifolium* Fern.			
E. hyssopifolium L.			
var. *linearifolium* (Walt.) Fern.			
E. verbenaefolium Michx.			
E. torreyanum Short			
E. altissimum L.			
E. rotundifolium L.			
var. *ovatum* (Bigel.) Torr.			
var. *lanceolatum* (Muhl.) Fern. & Grisc.			
E. sessilifolium L.			
var. *vaseyi* (Porter) Fern. & Grisc.			
E. perfoliatum L.			
E. rugosum Houtt.			
E. luciae-brauniae Fern.			
E. aromaticum L.			
E. incarnatum Walt.			
E. coelestinum L.	B. (4)	C. Hpr	D. 16
Kuhnia eupatorioides L.	B. (4)	C. Hp	D. 16
var. *corymbulosa* T. & G.			
Liatris squarrosa L.	B. (4)	C. Gst	D. 17
L. spicata (L.) Willd.			
L. microcephala Small			
L. graminifolia (Walt.) Willd.			
var. *smallii* (Britt.) Fern. & Grisc.			
L. scariosa Willd.			
var. *squarrulosa* (Michx.) Gray			
L. aspera Michx.			
L. sphaeroidea Michx.			
Grindelia squarrosa (Pursh) Dunal	B. (4), (2)	C. Hs	D. 16
Chrysopis graminifolia (Michx.) Ell.	B. (4)	C. Hp	D. 16
C. nervosa (Willd.) Fern.			
C. mariana (L.) Nutt.			
C. villosa Nutt.			
Solidago squarrosa Muhl.	B. (4)	C. Hs	D. 16
S. bicolor L.			
S. hispida Muhl.			
S. erecta Pursh			
S. roanensis Porter			
var. *monticola* (T. & G.) Fern.			
S. racemosa Greene			
S. speciosa Nutt.			
S. rigidiuscula Porter			
S. odora Ait.	B. (4)	C. Hp	D. 16
S. ulmifolia Muhl.	B. (4)	C. Hs	D. 16
S. juncea Ait.	B. (4)	C. Hsr	D. 16
S. boottii Hook.	B. (4)	C. Hs	D. 16

S. arguta Ait.			
S. harrisii Steele	B. (4)	C. Hsr	D. 16
S. patula Muhl.	B. (4)	C. Hs	D. 16
***S. strigosa* Small (*Gibson 168*, Adair County — F)			
S. nemoralis Ait.			
S. caesia L.	B. (4)	C. Hpr	D. 16
S. latifolia L.			
S. albopilosa Braun			
S. curtisii T. & G. var. *pubens* (M. A. Curtis) Gray			
S. rugosa Mill. var. *aspera* Ait.			
S. gigantea Ait. var. *leiophylla* (Ait.) Fern.			
S. canadensis L. var. *gilvocanescens* Rydb.			
S. altissima L.	B. (4)	C. Hsr	D. 16
S. shortii T. & G.	B. (4)	C. Hp	D. 16
S. graminifolia (L.) Salisb. var. *nuttallii* (Greene) Fern.			
S. rigida L. var. *glabrata* Braun	B. (4)	C. Hs	D. 16
S. sphacelata Raf.			
Astranthium integrifolium (Michx.) Nutt.	B. (1)	C. Th	D. 18
**Bellis perennis* L.	B. (4)	C. Hr	D. 14
Boltonia interior (Fern. & Grisc.) G. N. Jones	B. (4)	C. Hpr	D. 16
B. latisquama Gray var. *recognita* Fern. & Grisc.			
Aster divaricatus L.	B. (4)	C. Hsr	D. 16
A. macrophyllus L. var. *ianthus* (Burgess) Fern. var. *velutinus* Burgess			
A. schreberi Nees			
A. shortii Lindl.	B. (4)	C. Hs	D. 16
A. camptosorus Small			
A. cordifolius L.	B. (4)	C. Hsr	D. 16
A. lowrieanus Porter			
A. sagittifolius Wedemeyer	B. (4)	C. Hs	D. 16
A. drummondii Lindl.			
A. undulatus L.	B. (4)	C. Hsr	D. 16
A. puniceus L.	B. (4)	C. Hpr	D. 16
A. laevis L. var. *falcatus* Farw.	B. (4)	C. Hs	D. 16
A. laevis X *cordifolius*			
A. patens Ait. var. *gracilis* Hook. var. *phlogifolius* Nees	B. (4)	C. Hpr	D. 16
A. oblongifolius Nutt.	B. (4)	C. Hsr	D. 16
A. novae-angliae L.	B. (4)	C. Hpr	D. 16
A. prenanthoides Muhl.	B. (4)	C. Hsr	D. 16
A. concolor L.	B. (4)	C. Hp	D. 16
A. sericeus Vent.	B. (4)	C. Hs	D. 16

A. surculosus Michx.	B. (4)	C. Hpr	D. 16
A. dumosus L.			
var. *coridifolius* (Michx.) T. & G.	B. (4)	C. Hs	D. 16
A. vimineus Lam.			
var. *subdumosus* Wieg.	B. (4)	C. Hsr	D. 16
A. lateriflorus (L.) Britt.			
var. *angustifolius* Wieg.			
var. *pendulus* (Ait.) Burgess			
A. pantotrichus Blake			
A. paniculatus Lam.			
var. *simplex* (Willd.) Burgess			
A. pilosus Willd.	B. (4)	C. Hs	D. 16
var. *demotus* Blake			
var. *platyphyllus* (T. & G.) Blake			
A. umbellatus Mill.	B. (4)	C. Hpr	D. 16
A. infirmus Michx.			
A. linariifolius L.			
Erigeron pulchellus Michx.	B. (4)	C. Hsr	D. 16
var. *braunii* Fern.			
E. philadelphicus L.			
E. ramosus (Walt.) BSP.	B. (1)	C. Th	D. 18
E. annuus (L.) Pers.			
E. canadensis L.			
E. pusillus Nutt.			
E. divaricatus Michx.			
Seriocarpus asteroides (L.) BSP.	B. (4)	C. Hs	D. 16
S. linifolius (L.) BSP.			
Pluchea camphorata (L.) DC.	B. (1)	C. Th	D. 18
Antennaria parlinii Fern.	B. (4)	C. Ch	D. 12
A. plantaginifolia (L.) Richards			
A. fallax Greene			
var. *calophylla* (Greene) Fern.			
A. neglecta Greene			
A. solitaria Rydb.			
Gnaphalium obtusifolium L.	B. (1)	C. Th	D. 18
var. *micradenium* Weath.			
G. uliginosum L.			
G. purpureum L.	B. (2), (1)	C. Hsr	D. 16 (18)
Polymnia canadensis L.	B. (4)	C. Hp	D. 16
P. uvedalia L.			
Silphium laciniatum L.			
var. *robinsonii* Perry	B. (4)	C. Hs	D. 16
S. terebinthinaceum Jacq.			
var. *pinnatifidum* (Ell.) Gray			
S. trifoliatum L.	B. (4)	C. Hp	D. 16
S. incisum Greene			
S. integrifolium Michx.	B. (4)	C. Hpr	D. 16
S. perfoliatum L.	B. (4)	C. Hs	D. 16
Parthenium integrifolium L.	B. (4)	C. Hpr	D. 16
Iva ciliata Willd.	B. (1)	C. Th	D. 18
Ambrosia bidentata Michx.			

A. trifida L.			
var. *integrifolia* (Muhl.) T. & G. (Ballard County — Anderson, 1947. IA)			
A. elatior L.			
Xanthium chinense Mill.			
X. pennsylvanicum Wallr.			
X. italicum Moretti			
**X. spinosum* L.	B. (1)	C. Th	D. 7, 18
Heliopsis helianthoides (L.) Sweet	B. (4)	C. Grh	D. 17
var. *scabra* (Dunal) Fern.			
Eclipta alba (L.) Hassk.	B. (1)	C. Th	D. 18
Rudbeckia laciniata L.	B. (4)	C. Hs	D. 16
R. umbrosa Boynton & Beadle			
R. fulgida Ait.			
R. truncata Small	B. (4)	C. Hsr	D. 16
R. tenax C. L. Boynt. & Beadle			
R. triloba L.	B. (4)	C. Hs	D. 16
R. pinnatiloba (T. & G.) Beadle			
R. hirta L.	B. (2), (1)	C. Hs	
var. monticola (Small) Fern.			D. 16 (18)
Brauneria purpurea (DC.) Britt.	B. (4)	C. Hs	D. 16
B. pallida (Nutt.) Britt.			
Ratibida pinnata (Vent.) Barnh.			
Helianthus angustifolius L.	B. (4)	C. Hsr	D. 16
H. atrorubens L.	B. (4)	C. Hs	D. 16
var. *pubescens* Ktze.			
H. annuus L.	B. (1)	C. Th	D. 18
H. occidentalis Riddell	B. (4)	C. Hsr	D. 16
H. dowellianus M. A. Curtis	B. (4)	C. Hs	D. 16
H. glaucus Small	B. (4)	C. Hp	D. 16
H. microcephalus T. & G.			
H. decapetalus L.	B. (4)	C. Grh	D. 17
H. mollis Lam.			
H. divaricatus L.			
H. hirsutus Raf.			
H. maximiliani Schrad.			
H. grosseserratus Martens			
H. giganteus L.	B. (4)	C. Hp	D. 16
H. tuberosus L.	B. (4)	C. Gst	D. 17
H. strumosus L.	B. (4)	C. Grh	D. 17
Actinomeris alternifolia (L.) DC.	B. (4)	C. Hp	D. 16
Verbesina helianthoides Michx.			
V. occidentalis (L.) Walt.			
V. virginica L.			
Coreopsis lanceolata L.	B. (4)	C. Hsr	D. 16
var. *villosa* Michx.			
C. auriculata L.			
C. major Walt.			
var. *stellata* (Nutt.) Robins.			
C. pubescens Ell.	B. (4)	C. Hs	D. 16
var. *robusta* A. Gray ex Eames.			
C. tripteris L.			
var. *deamii* Standl.			
var. *intercedens* Standl.			

***C. verticillata* L. (*Philip Albion*, Jefferson County — KY)			
Bidens aristosa (Michx.) Britt.	B. (1)	C. Th	D. 18
var. *fritcheyi* Fern.			
var. *mutica* Gray ex Gattinger.			
B. polylepis Blake			
B. coronata (L.) Britt.			
var. *tenuiloba* (Gray) Sherff			
B. frondosa L.			
B. vulgata Greene			
B. comosa (Gray) Wieg.			
B. connata Muhl.			
var. *petiolata* (Nutt.) Farw.			
B. cernua L.			
B. bipinnata L.			
**Galinsoga ciliata* (Raf.) Blake			
Marshallia grandiflora C. L. Boynt. & Beadle	B. (4)	C. Hs	D. 16
Helenium tenuifolium Nutt.	B. (1)	C. Th	D. 18
H. autumnale L.	B. (4)	C. Hs	D. 16
H. nudiflorum Nutt.			
Dyssodia papposa (Vent.) Hitchc.	B. (1)	C. Th	D. 18
**Anthemis cotula* L.			
Achillea millefolium L.	B. (4)	C. Hsr	D. 16
**Matricaria inodora* L.	B. (1)	C. Th	D. 18
**Chrysanthemum leucanthemum* L. var. *pinnatifidum* Lecoq. & Lamotte	B. (4)	C. Hs	D. 16
**C. parthenium* (L.) Pers.			
**Tanacetum vulgare* L.			
Artemisia biennis Willd.	B. (2), (1)	C. Hs	D. 16 (18)
**A. annua* L.	B. (1)	C. Th	D. 18
**A. vulgaris* L.	B. (4)	C. Hs	D. 16
Erechtites hieracifolia (L.) Raf.	B. (1)	C. Th	D. 18
Cacalia suaveolens L.	B. (4)	C. Hs	D. 16
C. atriplicifolia L.			
C. muehlenbergii (Sch. Bip.) Fern.			
Senecio glabellus Poir.	B. (1)	C. Th	D. 18
S. aureus L.	B. (4)	C. Hs	D. 16
S. obovatus Muhl.	B. (4)	C. Hsr	D. 16
var. *rotundus* Britt.			
S. pauperculus Michx.	B. (4)	C. Hs	D. 16
S. plattensis Nutt.	B. (4)	C. Hsr	D. 16
S. smallii Britt.	B. (4)	C. Hs	D. 16
Arctium minus (Hill) Bernh.	B. (2)	C. Hs	D. 16
***A. tomentosum* Hill. (*Gibson 166*, Adair County — F)			
Cirsium muticum Michx.	B. (2)	C. Hs	D. 7, 16
C. vulgare (Savi) Tenore (Meade County — Davies. University of Louisville)			
C. virginianum (L.) Michx.			
C. altissimum (L.) Spreng.			

C. discolor (Muhl.) Spreng.
**C. arvense* (L.) Scop. B. (4) C. Gr D. 7, 17
**Onopordum acanthium* L. B. (2) C. Hs D. 7, 16
**Centaurea maculosa* Lam. B. (2) C. Hs D. 16
Serinia oppositifolia (Raf.) Ktze. B. (1) C. Th D. 18
**Cichorium intybus* L. B. (4) C. Hs D. 16
Krigia virginica (L.) Willd. B. (1) C. Th D. 18
K. dandelion (L.) Nutt. B. (4) C. Hrr D. 14
K. biflora (Walt.) Blake B. (4) C. Hs D. 16
**Tragopogon porrifolius* L. B. (4), (2) C. Hs D. 16

TABLE VI.—Summary of introduced species

Family	No.	Duration					Life-form				
	spp.	T	Sh	(4)	(2)	(1)	Ph	Ch	H	Cr	Th
Gramineae	38			16		22			13	3	22
Liliaceae	4			4						4	
Iridaceae	1			1						1	
Salicaceae	4	3	1				4				
Moraceae	3	2				1	2				1
Polygonaceae	8			4		4			4		4
Chenopodiaceae	3			1		2			1		2
Amaranthaceae	5					5					5
Aizoaceae	1					1					1
Portulacaceae	1					1					1
Caryophyllaceae	17			3	2	12		1	4		12
Ranunculaceae	3			2		1			1	1	1
Berberidaceae	1		1				1				
Papaveraceae	1				1				1		
Cruciferae	22			2	7	13			9		13
Rosaceae	8	1	4	3			4		4		
Leguminosae	19			5	5	9			9	1	9
Geraniaceae	2					2					2
Simarubaceae	1	1					1				
Celastraceae	1		1				1				
Malvaceae	6				2	4			2		4
Hypericaceae	1			1					1		
Umbelliferae	6			2	1	3			3		3
Primulaceae	2			1		1		1			1
Apocynaceae	1			1				1			
Convolvulaceae	3					3					3
Boraginaceae	6			2	2	2			4		2
Labiatae	18			12	3	3			15		3
Solanaceae	3		1			2	1				2
Scrophulariaceae	9			3	3	3			6		3
Bignoniaceae	1	1					1				
Plantaginaceae	1			1					1		
Rubiaceae	1			1					1		
Caprifoliaceae	1		1				1				
Dipsacaceae	1				1				1		
Compositae	23			10	5	8			14	1	8
Total:											
37 families	226 sp										

*_Taraxacum palustre_ (Lyons) Lam. & DC. var. _vulgare_ (Lam.) Fern.	B. (4)	C. Hr	D. 14
T. laevigatum (Willd.) DC.			
T. officinale Weber (Meade County — Davies, 1955. University of Louisville)			
*_Sonchus oleraceus_ L.	B. (1)	C. Th	D. 18
*_S. asper_ (L.) Hill.	B. (1)	C. Th	D. 7, 18
*_Lactuca scariola_ L. var. _integrata_ Gren. & Godr.	B. (2), (1)	C. Hs	D. 16 (18)
*_L. saligna_ L.	B. (2)	C. Hs	D. 16
L. canadensis L.	B. (2), (1)	C. Hs	D. 16
var. _integrifolia_ (Bigel.) Gray			
var. _latifolia_ O. Ktze.			
var. _obovata_ Wieg.			
L. villosa Jacq.	B. (1)	C. Th	D. 18
L. floridana (L.) Gaertn.	B. (2)	C. Hs	D. 16
L. biennis (Moench) Fern.			
Pyrrhopappus carolinianus (Walt.) DC.	B. (2), (1)	C. Hs	D. 16 (18)
*_Crepis pulchra_ L.	B. (1)	C. Th	D. 18
Prenanthes altissima L.	B. (4)	C. Hsr	D. 16
P. alba L.	B. (4)	C. Hs	D. 16
P. serpentaria Pursh			
P. trifoliata (Cass.) Fern.			
P. cylindrica (Small) Braun			
**_P. crepidinea_ Michx. (_D. V. Terrill_, Fayette County — KY)			
P. aspera Michx.			
Hieracium paniculatum L.			
H. scabrum Michx.			
H. gronovii L.			
H. longipilum Torr.	B. (4)	C. Hs	D. 7, 16
H. venosum L.	B. (4)	C. Hs	D. 16
H. greenii Porter & Britt.			

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Ecology of Some Earthworms With Special Reference to Seasonal Activity

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ABSTRACT: Earthworm activity is limited, rather generally, to certain seasons: in the monsoon tropical climate of Burma and in the humid subtropical climate of India, to 4-6 months of the rainy season, *i.e.*, some portion of May-October; in the humid continental climate of central Maine, to spring and fall months. Breeding, rather generally, is limited in India-Burma to a short period at end of the rainy season but in Maine to early spring and late fall. Exceptions, in each area, include limicolous species and individuals of other species in permanently moist sites. Some oriental species do not take advantage of artificially supplied moisture and become quiescent before end of the rainy season. Inactivity in India and Burma extends through hot and cold seasons. Peregrine species are more likely to remain active in exceptional sites and artificial conditions.

INTRODUCTION

Studies of the earthworm fauna of four areas, three prematurely ended and the other unlikely to be completed, provided the data that enabled the present contribution. The section on oriental species is from a manuscript written during tenure of a Guggenheim Fellowship. Most of the collecting in Maine was done by the writer for recreation and exercise during that Fellowship, while engaged in research financed by the Rockefeller Foundation and subsequently by the National Science Foundation or previously while teaching at Waterville. Several individuals have assisted in the collecting but especial thanks are due to Gerald Kinney for various interesting and important lots which otherwise would not have been secured.

RANGOON, BURMA

One sample of the data secured is presented in Table I. The species listed therein are the larger ones, but to them belonged a major portion of the 6000-odd earthworms secured during the academic year, June-March 1932-1933, in a sector of the Rangoon municipality centering at the biology building of Judson College. Collections were made by a laboratory steward in such hours as were free from more urgent duties. Each sort of habitat within the area was checked several times a month. Except on rare occasions, and then mostly after heavy rain, earthworms could be obtained only by digging.

The earthworm year in Rangoon usually begins, appropriately enough, in the same month as the academic year. All but two of the larger Rangoon species were represented in collections secured during June 1932. The absence of at least one species is noteworthy, as *Pheretima anomala* was not obtained in 1929-1933 until July —

TABLE I.—Numbers and stages of larger earthworm species collected in the Kokine Quarter of Rangoon during 1932-1933[1]

		Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Plutellus	pandus	7-0-2[2]	-13-20	-51-	-7-						
Drawida	abscisa	2-	6-	1-	-9-	-9-			7-		
	gracilis[4]	3-	27-	4-	3-			1-	1-	2-	1-
	longatria	16-	73-8-	29-0-21	39-0-23	1-0-3	-11	2-0-11[3]	11-0-16[3]	38-0-26[3]	59-0-48[3]
	papillifer	64-	72-1-	18-	49-0-19	1-	-2	-2	4-0-2		2-
	rangoonensis	2-	6-	5-3-	-9-	-5			1-		
	rara	70-	48-	-9	-13-10	144-0-12	9-0-1	2-	1-		
Lampito	mauritii	45-0-4	1-0-26	1-0-21	3-0-1	14-0-4	18-0-6	6-0-5	8-0-6	6-0-10	9-0-21
Pheretima	alexandri	2-	1-	3-0-7	-1	-7					
	anomala		19-	-37	-10	-38	-1				
	campanulata	2-	26-	14-0-6	2-19-137	-220	-14	-11	-1		
	elongata[5]	2-									
	houlleti	6-	23-18-12	14-0-24	3-7-23	-81	-18	-6	-6		
	peguana	38-3-	70-16-46	7-0-67	-63	-220	-13	-19	-6	-6	
	planata	2-	1-	24-	3-	-6	-10		-1		
	posthuma	2-	86-3-18	16-0-29	9-0-16	2-0-34	-10	-12	1-0-14	-4	-3
Perionyx	excavatus	40-0-15	10-10-14	23-0-16	-7	20-	9-	9-0-7	16-0-5	17-0-12	40-0-42
Octochaetoides	surensis	161-5-1	111-7-5	36-0-37	24-0-72	7-0-7	4-0-94	-39	7-0-161	27-0-161	5-0-55
Eutyphoeus	foveatus	159-	54-12-44	46-0-45	26-0-73	-22	-1				
	peguanus	82-	22-2-	3-0-3	11-0-11	9-0-19					
	rarus		14-0-6	-6	-12						
Pontoscolex	corethrurus	14-	-15	-5	-11	-51	-16	2-0-29	-29	3-0-16	8-0-9
Glyphidrilus	sp.[6]	8-	5-	3-	2-	5-			10-	11-	10-0-10
Rainfall in inches											
Normal		18.04	21.42	19.87	15.27	6.91	2.79	0.37	0.21	0.22	0.32
1932-1933		24.24	24.25	11.25	11.92	9.66	0.68	0.39	0.	0.	0.62

on the third of the month in 1931 but not until the seventeenth in 1933. However, in 1924, two specimens were found late in June.

Many species disappeared from strata of earthworm activity before the end of the academic year: In September, *Plutellus pandus* and *Eutyphoeus rarus;* in October, *Pheretima alexandri* and *Eutyphoeus peguanus;* in November, *P. anomala* and *E. foveatus* (only one specimen of each secured in that month); in January, *Drawida abscisa, D. rangoonensis, D. rara, Pheretima campanulata, P. houlleti, P. planata;* and in February, *P. peguana* (but only 44 specimens obtained in November-February as compared with 220 in October). These same species vanished, almost without exception, in other years. Variant times of disappearance for the academic year 1924-1925, as shown by regular sampling (5600+ specimens identified) from another and much larger portion of the municipal area were as follows: in October, *E. foveatus;* in November, *P. peguana, P. alexandri* and *E. peguanus* (only 4 specimens of the last two species found); in December, *P. anomala* (but only 13 specimens found in November-December); and in January, *D. papillifer.* Of that last species an occasional individual still could be found at Kokine in March, 1933, but through all the months after September only 13 individuals were found. Similarly, nine specimens of *P. houlleti* were obtained during February-March, 1924. After September, in each year, much more soil had to be dug over to secure fewer specimens of those species than in previous months. Activity clearly ends for most of these worms before November and nearly always, even for exceptional individuals, before the end of March. Not until late in May, at the earliest, were any of those species ever found again. By early June, earthworms were to be found almost everywhere although *P. anomala* appeared only in July.

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1 The year is divided in Burma into two major seasons: the rainy, May-October and the dry, November-March. The dry period is popularly subdivided into a cool (plains) or cold (hills) season, November-February and the hot season, March-May

2 The number of individuals collected in each of three recognized age classes: 7-, juveniles, without sex markings; -0-, aclitellates, with external sex markings but lacking a clitellum; -2, clitellates, clitellar development obviously under way or completed. Zeros are omitted whenever feasible.

3 Includes some postsexual individuals in which the clitellum has undergone more or less regression. Porophores and genital markings may also undergo some regression.

4 Clitellate specimens of *D. gracilis* never were found in Rangoon. One anterior portion of a clitellate individual was obtained from an unknown site elsewhere by a local collector.

5 *P. elongata* is very rare in Rangoon where soil conditions may be unsuitable. This exotic species flourishes, in India as well as Burma, in black earths and good cotton soils.

6 Identifications of species of *Glyphidrilus* (at least two) and of dwarf forms, those with a maximum thickness of 1-2 mm (of which 14 already are known to be present in Rangoon) had not been completed when war ended the investigation of Burmese earthworms locally.

Eight species were procurable through October-March, 1932-1933 and in other years during April-May. For each of those forms, as a species, there obviously need be no seasonally determined period of inactivity. Three species are restricted as to habitat, the glyphidriles to ooze and mud throughout the year, *Perionyx excavatus* to organic matter and to sites rich in manure, garbage, compost or other plant debris which must be moist. Four species are confined, from January to middle of May or later, to ghats where dhobies beat the laundry of the city against their rock slabs, small areas around wells and hydrants where people bathe, drainage ditches, margins of ponds, tanks, lakes, sites receiving waste effluents from bathrooms and cookhouses. The eighth species was found in the same period only in sand or sandy soil that remained moist. Water obviously is a major factor in controlling horizontal distribution during a considerable portion of the year and in that period continuation of activity for many individuals and several species is allowed only by such moisture as is accidentally provided at the surface of the soil by man. Monsoon moisture equally obviously, as a glance at the rainfall figures in the table will show, must be a major factor in controlling activity throughout most of the area. Considerable rain seems to be necessary, in the clays and iron-rich, laterite-derived soils of Rangoon, to enable return to activity. Not until late in a month with a normal rainfall of 11.98 inches do worms begin to appear. In May 1924, with a 2.44 inch deficit, *E. foveatus* was not found at all and even at end of the month other species were not common. In May 1925, with 5.41 inches more of rain, *E. foveatus* was readily obtainable almost anywhere and greater numbers of other species were active than in the previous year. Near saturation of the air during June-August might be expected to favor considerable activity on the soil surface. Castings, deposited there by species of *Eutyphoeus, Lampito* and some of the pheretimas, are obvious nearly everywhere one looks, but subterranean feeding and copulation seem to be the rule. Strayed individuals occasionally were seen wandering on the surface during daylight hours but only after heavy rain. However, *P. excavatus* must take advantage of the atmospheric moisture to explore the megadrile equivalent of outer space as it was found in trees and on roofs of buildings as high as four stories. Several of the small species that are not considered herein, dichogasters especially, also indulge in similar feats.

As the rainfall decreases and number of sunny hours increases in September, but more especially in October-November, soil that is not kept moist artificially dries. As it hardened the worms disappeared. Species of *Eutyphoeus* abandoned even the wet surface strata where *L. mauritii, Octochaetoides surensis* and *Drawida longatria* appear to aggregate. The wide-wandering *P. excavatus* often finds refuge during the drouth in submerged vegetation. Least moisture seems to be required by *Pontoscolex corethrurus* but eventually worms of that species empty the gut and, each coiled tightly into a ball

within a closed chamber several inches below the surface, remain for an unknown time in a state sometimes called diapause. That term is used hereinafter for worms in the condition just described but without reference to any other characteristic such as water content.

Reaction to seasonal decrease in precipitation accordingly varies interspecifically as well sometimes as intraspecifically.

All worms secured in June 1932, except a few individuals of four species, were juvenile. Only in July or even later were adults of other species obtained. Records still available for 1933 show that in the same area clitellate specimens were first secured as follows: Early in June, *L. mauritii.* Last week of June, *Plutellus pandus.* In July, *Pheretima peguana* in the first week, *E. foveatus* on the 7th day, *O. surensis* on the 14th, *P. posthuma* on the 16th, *E. rarus* on the 20th, *E. peguanus* on the 23rd, *Drawida longatria* and *P. houlleti* in the last two weeks. In August, *D. rangoonensis, rara, P. alexandri, P. anomala* (on the 17th) and *P. campanulata.* In October, *D. papillifer* and *P. planata.*

Appearance of the first macroscopically recognizable epidermal differentiations that allow a specimen to be listed as clitellate, does not, of course, show that the worm is ready to breed. One to several additional weeks may be required. Maximal tumescence of the clitellum doubtless is correlated with full maturity, but whether the yellow, orange or red coloration that may become visible in the thickened epidermis is associated primarily with function or regression is unknown. Definite dates for beginning of breeding cannot now be stated, but in most individuals of many species sperm were not accumulated on male gonoducal funnels ready for discharge during copulation until late in August or early in September. Breeding of terricolous species must then be limited rather generally to the period from the middle of July to the middle of October, but for many individuals of most of these forms to several weeks in September. Breeding, so far as could be deduced from presence of a seemingly functional clitellum, appeared to be possible at any time for *Perionyx excavatus, L. mauritii* and *O. surensis.* Confirmation for *P. excavatus* was provided subsequently by finding individuals with aggregated sperm on male gonoducal funnels in every month of the year. Cocoon deposition in the laboratory during December-January and the finding of cocoons outside from September until the end of March hints that *Pontoscolex corethrurus* may be similarly uninhibited. During nine months of the year at least, *Pheretima posthuma* is able to breed but cocoons were not deposited in the laboratory and there the clitellum soon disappeared. Glyphidrile cocoons were found only during March-April. However, uninterrupted breeding of these limicolous species is indicated by size of juveniles that were obtained throughout the year.

Individuals of five species, *D. longatria, O. surensis, Perionyx excavatus, L. mauritii* and *Pheretima posthuma* remained active, in favorable conditions, after the clitellum had regressed. Late in May

or early in June some few specimens of those species usually could be found with the marks of regression still recognizable. Accordingly, a second breeding season for such individuals as survive the drouth seems possible but has not yet been demonstrated in laboratory controls.

Of the early disappearing species, *P. pandus, E. foveatus, E. peguanus* and *E. rarus* are endemic. Of the species that are active into March, *D. gracilis, D. longatria, D. papillifer* and the glyphidriles are endemic. The others, *O. surensis, Perionyx excavatus, L. mauritii, Pheretima posthuma,* and *Pontoscolex corethrurus,* like most of the omitted small species, are exotic and were introduced by man. No information is available as to seasonal periodicity in their original homes some of which are unknown.

BURMA

Several hundred thousand Burmese earthworms collected outside of Rangoon in 1922-1940 provided data that enable the following generalizations. From the southernmost tip of the country to the foothills of the Himalayas, the rainy season is the period of activity for terricolous earthworms. On the Shan Plateau, at elevations of 4000 feet and more, casting deposition on the surface, especially by giant species of *Tonoscolex* (Gates, 1927) testified to much ingestion of soil during May. Contrariwise, similar activity in the dry zone of central Burma was recognized later than in Rangoon. However, on the porous soil of that zone less precipitation seems to stimulate the worms sooner. Thus, after the first seven days of rain, characteristic tower-like castings in great abundance dramatically demonstrated almost over night that feeding had begun again by species of *Eutyphoeus.* In the western hills, Dr. G. Heinrich was able to find specimens of the same genus after only two rainy days. Duration of activity accordingly may be shortened or lengthened locally by soil structure, elevation and variation in amount of precipitation. Species of *Eutyphoeus* disappear toward end of the rains just as in Rangoon; in Akyab for instance, the earthworms disappeared even during September and October with 22 and 11 inches of rain, respectively. Occasional individuals of other endemic forms may remain active for several more weeks especially in dense jungle shade, under accumulations of litter and in other sites where for one reason or another soil dries less rapidly. Horizontal distribution during the latter part of the dry season is markedly discontinuous as in Rangoon and activity is restricted to strata that remain wet and restricted in part because of human activity. Worms found at such sites in January-April are apt to be mostly exotic. Endemics usually are referable to species of *Drawida.* Foreign species, in addition to those already listed from similar sites in Rangoon, include Chinese forms and one lumbricid supposedly from northeastern United States.

Breeding, as evidenced by maximal tumescence of the clitellum and by aggregated sperm on male funnels, rather generally through-

out the country and certainly for most individuals of many terricolous species, is restricted to a single period centered in September. At higher elevations, in a northern portion of the Shan Plateau, the reproductive period may be quite definitely later in the calendar year, possibly because of the lower temperatures. Maturity, in most of the medium-sized species, probably is attained during the breeding season of the next year. Giant species of *Tonoscolex* in the lowlands, according to available evidence, cannot be expected to breed even at end of the second year, possibly not until the fourth.

The limicolous glyphidriles are known to be active on the Shan Plateau through the dry season and in the lowlands of the mid-longitudinal third of Burma during the rains. Destruction of records and collections during World War II prohibits any statement as to breeding except that in Victoria Lake cocoons were deposited on or above the surface of the bottom ooze. Some at least of the hatchlings must feed for a time near the banks before moving to sites that were not investigated.

Two sorts of unusual activity also are seasonal. "Mass migrations" were not seen by the author but they often have been observed by government officials and missionaries while traveling along the mule tracks of the western hills. All written and oral reports agree in the following particulars.—At the beginning (October-November) of the cold season, in a region where mountains are covered with a thick undergrowth of mosses and ferns, worms crawl on the surface early in the morning in huge numbers. As they drop down from the upper bank they almost cover the road. Direction of travel, whether on the track or at either side, is always downhill. In the evening not a worm is to be found.—The assumption usually made was that the annelids were in search of more adequate supplies of water. A number of migrating individuals were preserved. All were referable to the genus *Perionyx* but were immature and could not be further identified.

"Mortal wanderings" have been observed, sometimes for several days in succession, only after the rains had ended and, indeed, after activity in the hardening soil rather generally had ceased. Hours of emergence are unknown but the wanderers were found, early in the morning on roads, paths, in almost any open place. Sooner or later locomotion ceased and the worms dried up. Individuals that were preserved proved to be fully mature. All of them belonged to endemic species of *Eutyphoeus, Desmogaster* or *Pheretima* some of which have been collected but rarely. One desmogaster, except for several individuals, is known only from wanderers that happened to be above ground when someone in the vicinity was looking for them. Residence of these rather large worms, at greater depths than were dug over or in soil made impervious to cooly implements by interlacing roots of the rainforest, may be responsible for failure of various attempts to secure material.

During the rains, almost everywhere, in the hills, the plains, even

in the dry zone with only 20-40 inches of rain, earthworms are present in great profusion. Multitudes, in certain parts of the country, do die on the surface early in the dry season but in the next southwest monsoon worms are just as common as previously. Few resting individuals were found in spite of visits at every opportunity to sites where earth was being moved. However, exposed surfaces never were close to the water table.

Everyone in Burma who has given the matter any thought or who has heard comment on earthworm reappearances is sure that the worms go down deep in the soil at end of the rains. Those who dug wells during the dry weather reported finding aggregated earthworms near the water table. The mass always was characterized as a "ball" and its thickness was variously estimated to be six to twelve inches. Such balls never became available to the author for examination. However, live worms placed individually in the same receptacle always aggregated, regardless of species differences, in a closely intertwined cluster that often required some effort to disentangle. A clump of a dozen or so specimens has been observed on countless occasions, in the laboratory and after appropriate stimulation, to assume a shape comparable to that of a ball. Similar but possibly larger clumps were said by various individuals to have been seen in heavily flooded areas. There are then good reasons, including some not mentioned above, for believing that many Burmese species do pass the drouth in more or less tightly clustered aggregations.

Hibernation and estivation are not strictly applicable in Burma as the period of inactivity comprises both cool or cold (according to elevation) and hot seasons (*cf.* Footnote 1, Table I).

ALLAHABAD AND NORTHERN INDIA

Our knowledge of the earthworm ecology at Allahabad comes from a thirty-month survey that provided some 25,000 specimens and more especially from the 15,000 that were obtained by regular collecting, weekly during July-November 1943 and fortnightly during December-May 1943-1944. Some of the results of that study already have been published (Gates, 1945, 1947).

The earthworm year begins at Allahabad in July, at least one month later than in Rangoon. By the end of September the worm population near the surface already was decreasing. From the first of October more hours increasingly had to be spent in digging to secure fewer specimens than previously and by the end of the month three species had disappeared. Two more vanished in November and only 16 specimens of *Eutyphoeus* (2 species) were obtained in December. Even the exotic *L. mauritii* which flourishes during the hot months in artificially wetted habitats of arid central Burma was not to be found at Allahabad in January-June. For seven endemics including the three species of *Eutyphoeus,* three to four months of activity are followed by eight to nine months of inactivity. As the worms are quiescent during both cold and hot seasons, hibernestiva-

tion, or some other words expressing the same idea, alone is applicable. The only resting individuals secured, juveniles of *Bahlia albida,* were in diapause, each within a small closed chamber in the upper three inches of soil. Major trunks of the vascular system were distended with blood that appeared not to be circulating. Immersion in water (April) straightened the worms almost at once but did not bring them back into activity.

From October through May, earthworms increasingly were restricted to sites by running and standing water or to those that were kept wet by man. In June of 1943 as well as of 1944, a few individuals still could be found but only at one place, between joints of a pipe that was under water in a ditch. Even those species that linger on after December, whether intruders from the adjacent Deccan or introduced by man, must rest, at Allahabad, during some portion of the year.

Endemic species were not mature in July though seven clitellate specimens of *E. incommodus* were obtained in that month. Sexual individuals, clitellate and with sperm aggregated on male funnels, of *E. incommodus* were found in the first week of August, of *E. waltoni* on August 16 and of *E. nicholsoni* on August 26. Copulation continued, for *E. nicholsoni* and *E. waltoni,* into November. Breeding, as at Rangoon, is centered in some part of September. Adults of *E. incommodus* that had been clitellate and presumably had bred in the previous rain season, were recognized early in July. Life ends, however, for many mature individuals of *E. nicholsoni* and *E. waltoni* in October-November when they are dried by the sun as they wander on the surface in the morning. Again, as in case of mortal wanderings in Burma, these worms showed no macroscopically recognizable indications of disease and were not heavily parasitized.

Other species (perhaps with one exception), according to evidence provided by clitellar tumescence, brilliant spermatozoal iridescence on male funnels, laying and/or presence of hatchlings, breed from July well into the next calendar year. Sexual individuals of five taxa were found as late as the first week in May. Clitellate individuals of the exceptional species, *Plutellus exilis* (presently unknown outside of a single Allahabad quarter), were secured only in November-April and at sites too deeply flooded to be investigated during the rains. Breeding then may be possible, in appropriate conditions, for these species throughout the year. Postsexual active adults of the larger species were obtained from August to May. A second period of breeding appears to be possible for most of the kinds that are thicker than two millimeters but whether any particular individual can breed twice within a single year was not learned.

In the Gangetic alluvial soils of Allahabad, with a pH in the vicinity of 7.5, earthworms appear to be common everywhere during the rains. The three species of *Eutyphoeus* advertise their presence throughout nearly all of the area by erection of tower-like castings. Habits of three other geophagous endemics are unknown. Five ex-

otics also are geophagous but only *L. mauritii* testifies to a wide distribution by characteristic non-tower-like castings. Rarity of one exotic may be due to more recent introduction and two others were found only or mostly (*P. houlleti*) in earth around roots of potted plants. The fifth form, *P. posthuma,* confines itself largely to sands of river banks on which characteristic pellet-like castings are deposited.

The remaining species, including *Plutellus exilis,* are entirely or mostly confined to accumulations of organic matter such as manure, dumps, sites receiving kitchen drainage, ditches carrying waste effluent of human habitations, etc. The single lumbricid was found only at such sites and in flower pots. Little is known about this species, *Bimastos parvus,* in its supposed North American home perhaps because it is primarily a litter-feeding species in some forested region of the great portion of the continent where earthworms never have been collected. A few individuals of geophagous species were found in organic sites. Strays of two organic feeders were found in ordinary soil along with geophagous species.

The humid subtropical climate of Allahabad differs noteably from the monsoon tropical climate of Rangoon in precipitation (*ca.* 40 versus *ca.* 100 inches) and in temperature (colder in October-March and hotter in April-June). Most of the rain at Allahabad likewise is monsoonal but falls during June-September. The five inches of June rain is insufficient to bring worms back to the surface and reappearance in July is gradual rather than dramatic. Greatest activity is during the three months with averages of 12, 10 and 6 inches. October has 2 inches but other monthly averages until June are less than an inch and of no significance to earthworms.

Species of *Eutyphoeus* vanish at end of the rains in Rangoon which is near the eastern boundary of the generic range and also at Allahabad which probably is as near the western boundary of a natural generic range that has been extended somewhat because of transportation by man. All available evidence indicates uniformity throughout the genus. These species were much easier to find during October-November at Allahabad with a rainfall of scarcely three inches than at Akyab and Rangoon with precipitations in the same months respectively of 16 and 9 inches.

No glyphidriles were secured in Allahabad by considerable digging although a very few, all young juveniles, were found in adjacent areas. However, at one site on a river bank in the Himalayan Terai, 135 specimens (110 clitellate) were obtained late in October but only at a depth of 18 inches. Lack of collections from similar depths at appropriate sites presumably was responsible for failure to secure clitellate individuals in the Kokine quarter of Rangoon. *D. gracilis,* in the adult stage, now also seems likely to have been restricted to strata not usually investigated in Burma.

The earthworm year, in the Allahabad sector of the Gangetic Valley, in the Terai and the Dun as well as the Himalayas, so

far as could be learned from wartime observations and collections, also comprises a single period of activity followed by one of quiescence. Duration of each presumably is determined primarily by the climate though postponement of quiescence may be permitted at various sorts of sites and especially at those kept moist by man. To the west, in the plains of the Indus Valley, indigenous species are unknown. The pauper fauna comprises exotics introduced from other parts of Asia (including peninsular India), Malaysia, Europe and America. Further observations and comments on the earthworms of west Pakistan and adjacent portions of Hindustan are omitted as a survey now under way in Lahore is expected to provide more substantial support for interesting conclusions.

The Malay Peninsula

This area has a humid, equatorial climate commonly said to be characterized by a constantly high temperature and heavy rainfall throughout the year. The range of annual temperatures at Singapore is only 3-4° F. and monthly rainfall is 6-10 inches. In such circumstances one might expect earthworms to be as common all the time as in Burma during the rains and activity to be possible for terrestrial as well as limicolous species throughout the calendar year. Nevertheless, earthworms were hard to find at Singapore and vicinity on several occasions and no evidence of widespread casting deposition was recognized.

Although annual temperature ranges are slight, the diurnal may be as much as 15-20° and at Singapore the recorded maximum and minimum temperatures, 97° and 66°, are not far from those of Rangoon. Alternating periods of activity and quiescence, though possibly with less regularity than in monsoon climates, now are anticipated but destruction of records during World War II obviates presentation of supporting data.

Maine, United States

A few scattered records of several species, some without locality or other data, constituted hitherto our knowledge of the earthworm fauna of this state. As a result of a study that is still under way, 22 species can be listed from Maine. All are present in the central portion of the state that is now under consideration. Eight, found during twelve years search only in greenhouses and conservatories, need little further mention in a contribution primarily concerned with natural climates. Frequent, regular sampling of various sorts of habitats, as at Rangoon and Allahabad, was impossible throughout any single year but the same or adjacent sites have been examined, as often as circumstances permitted, over a period of six or more years. Except as otherwise noted, worms were obtained by digging. Such disturbance of the habitat may have exterminated isolated colonies of rarer species. Chemicals, including potassium permanganate, were used on several occasions. Where needed, data from

collections made by or for the author in other states are cited from unpublished records.

Allolobophora chlorotica, except for two juveniles, was found only in and around gardens, in a dump where garden refuse obviously had been deposited, in outside beds of greenhouses, in five sets of greenhouses at Bangor and Ellsworth. All worms were of the green variety. Nearly as many specimens were obtained from the greenhouses as from all outside sites. Active individuals were obtained outdoors in April-May, October-November (June-July, Massachusetts and Vermont), in greenhouses November-March (August, New York State). Year round activity obviously is possible for the species.

Clitellate individuals were secured outdoors in April-May, October-November (June-July, Massachusetts and Vermont), in greenhouses November, February, March (August, New York State). In each of those months some of the worms were fully clitellate and, as proved by presence of sperm on male funnels and in spermathecae, able to breed, *i.e.,* lay or deposit cocoons (sometimes called capsules by laymen and oothecae by zoologists). Spermatophores, 1-6 per worm, were noticed only in April. These bodies, adhering to the cuticle, seem to be characteristic in the family (Lumbricidae) to which all our outdoor species belong. Lumbricid spermatophores have no function. They were found frequently in the killing fluid and are rubbed off soon after copulation. Their presence on a worm then is proof of recent mating. For this species, year round breeding seems to be possible in appropriate conditions.

Resting individuals were not found, but estivation and hibernation must be necessary in Maine at outdoor sites.

Allolobophora longa has been found more often than *A. chlorotica,* not only in turf, lawns, gardens and flower beds but also in some fields and pastures further from habitations, in soil of flower pots from private residences as well as in four sets of Bangor greenhouses from one of which it was secured several years in succession. Active individuals were found outdoors in each month of March-December; postsexual aclitellate adults in March, April, June, August, October and November; clitellate adults in April-May as well as the first few days in June, October-December; aclitellate adults in April-July and September-October; juveniles in April-December and in greenhouses November-February. Year-round activity obviously is possible for the species. Active worms collected between the middle of June and the end of September were from the following sites; under turf of a copiously watered lawn (September), densely shaded and wet litter (August), a gulley with water (July), swampy river banks. In open areas not artificially supplied with water no worms were found during the summer.

Spermatophores were seen in October-December and in April, in the latter month on one worm from a site where the ground still was frozen at a depth of an inch. Six of seven clitellate speci-

mens secured October 13 had no spermatophores. Five of the worms, of course including the one with spermatophores, had copulated and presumably were ready to lay. The other two, as indicated by the massed sperm on male funnels, were ready to copulate but had not yet done so. Each of 22 clitellate specimens secured November 19 from the same site had copulated. Sperm not extruded during breeding presumably are lysed as none has been found in postsexual aclitellates at end of hibernation or estivation. The single active clitellate worm secured in September (from watered turf) was not in condition to copulate or reproduce.

Although year-round activity seems possible, in appropriate conditions, breeding cannot yet be so characterized. As postsexual worms can be arranged in series, decreasingly showing evidence of previous functioning to early stages of spermatogenesis, individuals that presumably had layed in the previous season should again be able to reproduce.

Juvenile and postsexual worms in diapause were found during September 2-3 inches below the soil surface of open areas. Hibernating individuals have not yet been found at any level.

Allolobophora tuberculata probably is the most common species in Maine where it has been found in peat (the only species), manure (once), under cowpats in pastures, in hen and cowyards, matted leaves, compost, city dump, on city roads and sidewalks in spring after heavy rain, in swampy brook and stream banks, river banks, leaves and mud under two feet of water, under logs in stream beds, in turf, lawns, gardens, pastures, fields, forests, 11 sets of greenhouses at Orono, Bangor and Bar Harbor. Active individuals were found outdoors April-December and in greenhouses October-March. Year-round activity obviously is possible for the species. Most of the active worms secured June-September were from damp or wet sites. Gardens provided a very few specimens in July and September but searching in other open areas was fruitless.

Juvenile and clitellate worms were obtained in every month of the year, postsexual aclitellates in each month except February. Spermatophores were noted April-May and October-December. Copulation was seen only in the spring. In one clitellate sample of an October 13 collection, 25 worms (9 with spermatophores) were able to breed and the remaining 9 were ready to copulate. In a similar sample from an October 20 collection at the same site 26 worms (11 with spermatophores) were able to breed and the other four were ready to copulate. All dissected specimens from a November 19 collection at the same site were in a condition to lay. Certainly, most of the breeding of this species in Maine, because of more limited activity in other seasons, is during April-May and October-December. In the forests of Piscataquis County where the season on June 27 was at least a month later than in Bangor, worms were not yet mature enough to copulate.

Estivating worms found several inches below soil surface of open

fields in September were in a state of diapause. Resting worms at other sites, in the upper four inches of soil in summer but much deeper down in winter, were damaged by the machinery that exposed them. Movements of estivating worms (perhaps not in diapause) hinted that those animals, if not mutilated, could have crawled away immediately on exposure. A second breeding season for particular individuals was indicated by the same evidence as for *longa*.

Allolobophora turgida is not common but has been found more often than *A. chlorotica* and in compost, leaf litter, waste land, at the city dump, a stream bank, a river bank, a pasture spring near a farmhouse, turf from a lawn (1 specimen), sidewalk after rain (1 specimen), abandoned grape arbor (1 specimen), flower beds, gardens, outside greenhouse beds and in four sets of greenhouses at Bangor, Ellsworth and Bar Harbor. Samples of more than 20 specimens were obtained only from two flower beds, a long abandoned garden site, one compost heap, the city dump and moist humus in the University of Maine forest at Orono. Except at that last site, the stream bank and the pasture spring, each colonization obviously can be attributable to transportation by man. Active individuals were found outdoors April-June and August-December and at greenhouses in January. Nearly all of the June-September specimens were from sites that were moist or wet. Year round activity is possible, in appropriate conditions, for the species.

Clitellate individuals were found April-June, August, October-December and in January at a greenhouse, June and August specimens in brook and river banks. Spermatophores were noted April-May, August and October. Copulation was seen only in the spring. Dissections of clitellate samples show that some worms were ready to breed in each of the months during which the species was found.

The only estivating specimen secured (September) was in a state of diapause. Hibernating specimens, from the site of a former garden, were obtained at greater depths but were considerably mutilated by the machinery that exposed them.

Dendrobaena octaedra is rare in central Maine where it was found only at twelve places, three in Bangor, two in Dedham and one each in seven other townships. Sites were swampy stream and brook banks, under elm logs, in leaves of roadside gulleys and ditches with water, compost (1 specimen), in and under leaf litter in woods. Prior to the present study this species had been found by the author in manure piles of several counties. Although two samples were from forests in unsettled sections of Piscataquis County, both were from vicinity of former habitations to one of which exotic plants are known to have been introduced by a well-to-do man locally reputed to have been a smuggler. Presence at some of the other sites obviously is attributable to transport by man. Active individuals were found, in April-October, at a site that has been under observation for eight years and were secured from localities outside

Maine in November-December. Year round activity presumably is possible for the species where conditions permit.

Clitellate specimens were obtained in April-August and October. Cocoons were deposited in damp leaf litter during July-August. Reproduction is parthenogenetic.

Quiescence during the winter in Maine obviously is necessary and a juvenile found in aggregated silty clay dug up from unknown depths after the ground had frozen in November probably was hibernating.

Dendrobaena rubida was found more commonly and in larger numbers than *D. octaedra,* in sandy loam four and one-half feet below ground level in unfloored cellar of a dwelling house, in toilet bowl of another residence, black earth of brook and stream banks, saturated soil around a pasture spring, under logs in a pasture, under elm logs, under stones in woods, in cowyards, manure piles, powdery black soil where manure formerly had been piled, compost, matted leaves at a dump, leaf litter and humus in forests, culture beds of an earthworm farm and six sets of greenhouses in Orono, Bangor and Ellsworth. Active individuals were found outdoors April-December and in greenhouses October-March. For this species year round activity, in appropriate conditions, obviously is possible.

Clitellate individuals were found outdoors April-December and in greenhouses October-February. Spermatophores (containing sperm) were found on outdoor worms April-May and October-December, on greenhouse worms October-March. In each of the months in which clitellate worms were obtained, presence of sperm on male funnels, and in seminal receptacles as well as the clitellar tumescence, indicated readiness to lay. Breeding certainly appears to be possible through so much of the year as temperature permits.

Quiescent individuals were not found, but at some of the sites hibernation within the soil is probable. The owner of the cellar mentioned above insisted that entrance could have been gained only by burrowing down from the outside and then under the foundations of the house.

Parthenogenetic morphs of the species are present in central Maine but more rarely and in fewer numbers.

Eisenia foetida, the brandling, was secured from manure, compost and matted leaves at 12, 3 and 4 sites respectively and in 6 sets of greenhouses at Bangor, Ellsworth and Bar Harbor. Active individuals were found outdoors March-July and September-November. Some were clitellate in March, May, July, October-November. This species is raised for sale at three "earthworm farms" in central Maine. Breeding, as indicated by maximal clitellar tumescence, presence of sperm in seminal receptacles as well as on male funnels and by cocoon deposition, is year round for the species in habitats providing appropriate temperature, moisture and food.

The local distribution obviously is in part due to human activity but some of the finds seem to indicate a propensity for wander-

ing. Several months after departure of a circus the species was found in a pile of elephant droppings. The nearest site at which other specimens could be found was a greenhouse manure pile more than a quarter of a mile away. One individual entered a leaf-filled open wood box held six inches above the ground by stones. Artificial fertilizers had been used in nearby gardens and flower beds where *E. foetida* was not found. Again the nearest known site was a greenhouse but this time a mile away. However, some of the gardens in the intervening area could have been manured.

Eisenia rosea seems to be nearly as common as *A. tuberculata* and was found in forests, fields, pastures, cowyards, gardens, lawns, on roads and sidewalks after heavy spring rain, in a city dump, waste land, under rocks and logs in open areas, in compost, in and under matted leaves and at 8 sets of greenhouses in Orono, Bangor, Ellsworth and Bar Harbor. Many of the sites were unusually damp for the season or even saturated but others appeared to be rather dry. Active individuals were found outside during April-December and in greenhouses October-March. Year-round activity again seems possible for the species where external conditions permit it.

Clitellate adults were secured outside, April-July, September-November and in greenhouses October-March. Cocoons were not found. A yellow coloration of the clitellum that persists as tumescence disappears may prove to be associated only with regression after breeding has ceased. The species is represented in central Maine, so far as could be discovered, only by male sterile morphs. As reproduction must be parthenogenetic the only available evidence of readiness to lay, until the ovaries can be studied, is that provided by the thickness of the clitellar epidermis. Assuming then that near maximal or maximal tumescence of the clitellum does indicate ability to lay, breeding appears to be possible, for the species, throughout the year.

Resting individuals were not found though hibernation and estivation must be necessary for much of the population.

Eiseniella tetraedra is uncommon in central Maine where it usually was found in mud under water or in saturated soil (black) of stream, brook and lake banks. One colony is present in the mud around a pasture spring far from any brook or pound but fairly near a farmhouse. A few individuals, one in a flower bed outside a Bangor greenhouse and three under elm logs in a well drained pasture, appear to have strayed from their usual habitat. Four specimens were found in an Ellsworth greenhouse.

Active individuals were obtained in April-July and October. Clitellate adults were secured in May-July. Spermatophores, all without sperm, were found on four worms in March and one in June. Scattered specks of iridescence on male funnels showed that few sperm had been matured. The species is represented in Maine only by an athecal morph. Parthenogenetic reproduction is probable.

Resting individuals were not found but subsequent reappearances

at a site from which all active worms had been removed may be indicative of existence of a quiescent stage.

Lumbricus castaneus is fairly common in central Maine where it was found in and under matted leaves at a city dump, leaf litter and humus in woods, leaf piles, in leaves of roadside gulleys and ditches with water, in compost, manure (once), finely powdery black soil near a manure pile, cowyards, under timber and cowpats in pastures, stones, logs, in saturated soil by pasture spring, in saturated black soil of stream and brook banks, in turf of lawn (2 specimens), in cellophane-wrapped lettuce purchased at a supermarket December 23, in a flower pot at a residence, in outside beds of greenhouses and in four sets of greenhouses at Orono, Bangor and Ellsworth. Active individuals were found outside, March-December and in greenhouses October-March. Year round activity, in appropriate conditions, obviously is possible for the species.

Clitellate individuals in a breeding state were secured outside, March-December and in greenhouses during March. Year round breeding, in appropriate conditions, seems possible for the species.

Hibernation must be necessary at many of the sites. Active clitellate specimens from aggregated silty clay recently dug up from unknown depths after the ground had frozen probably had been quiescent. These worms and a juvenile of *Dendrobaena octaedra* or their ancestors may have been taken to the cemetery along with some of the numerous potted plants.

Lumbricus rubellus is rare in central Maine where but 36 specimens were found at seven places during the last twelve years. Sites were swampy stream bank, under cowpats in pasture some distance from farmhouse, under stones and boards in cowyard near another farmhouse, in moist humus and litter of the University of Maine forest, a garden and one city street after a heavy rain in October (2 specimens). Active individuals were found in June-July and October-November. The July worms were from damp soil in Piscataquis County forests but near sites of former habitations.

Clitellate individuals, in a condition to lay, were found in June-July, October-November and in other states (Gates, MS) during March-May, September and December. For this species breeding appears to be possible, in appropriate conditions, throughout the year.

Resting individuals were not secured but hibernation must be necessary at each of the Maine sites.

Lumbricus terrestris, the dew worm, night-walker or night-crawler, probably is about as common as *A. tuberculata*. it has been found in aggregated silty clay, fine powdery black soil, sandy loam, sand mixed with organic matter and in weathered glacial debris primarily from shales and granitic materials. Sites include almost every open area such as lawns, gardens, fields, pastures, bare ground, waste land by river, golf greens and golf courses, also on city streets and sidewalks in April, May and November after heavy rain, in saturated

soil by brook and stream banks as well as by a pasture spring, in a cellar (cf. *D. rubida* above), under stones and elm logs, in cow-yards, leaf piles, matted leaves at city dump, compost, under cow-pats in pastures, in culture beds of an earthworm farm and in five sets of greenhouses (juveniles only) in Bangor and Bar Harbor. Of 317 specimens secured from under cow pats and in other organic matter, 20 were adult and 297 were juvenile. Thirteen of the adults were in a breeding stage and only one of them was found in each of the sites. Cocoons were not found in the organic materials in which juveniles now appear to aggregate after hatching.

Clitellate individuals in a condition to breed were found outdoors in March-December. Copulation was noted every time worms were seen in activity at the surface during the night. Active juveniles were found in greenhouses during November-March. Breeding presumably could be, in appropriate conditions, year round for the species.

On hot and dry summer nights these worms do not come to the surface unless the turf is watered but they do emerge as soon as dew or fog provides the required moisture. Presumably then, estivation is inapplicable to the state of worms that have only temporarily withdrawn to unknown depths. Enforced cessation of activity at the surface in the winter perhaps can be called hibernation until it has been possible to learn just what happens at that time. Activity at the surface is resumed, as noted below, while the soil is still frozen.

Octolasium cyaneum, previously known in North America only from a Boston garden and arboretum, is very rare in central Maine where 37 specimens were obtained at six sites, five of which are in Bangor. Habitats include grape arbor of an abandoned estate, flower bed, in or adjacent to a long abandoned garden and two sets of greenhouses (13 specimens). The sixth site, in Dedham, is a leaf pile beside the camp of owner of the Bangor garden. Active individuals were found outside, April-May, August (ground damp, bare and completely shaded from direct sunlight), October-November, in greenhouses October and January. Clitellate individuals were found in May, August, October-November. Reproduction is parthenogenetic.

Hibernation is necessary at each of the sites and estivation at some of them.

Octolasium lacteum is not as rare as *O. cyaneum,* having been found at one place in each of nine townships. Sites include a garden (once), humus in University of Maine forest, clayey soil in forest cutting, in mud near cat tails by lake, in brook and stream banks. Except at two places, one of which is a garden, the sites were damp to saturated. However, a second Orrington site was in a very dry, alder overgrown pasture where two specimens were obtained in October.

Active clitellate individuals were secured in May-July, September-

October and outside Maine in August and November. Reproduction is parthenogenetic, at least in Maine, because of male sterility.

Hibernation is necessary at each of the Maine sites. Sampling may have exterminated certain colonies but estivation is anticipated for worms in such places as do not remain wet during the summer.

DISCUSSION

Any earthworm fauna native to Maine was exterminated during the ice ages. All outdoor species are exotic, of north European origin and doubtless were introduced since 1492. Indeed, persons now living remember when earthworms were unknown in their Aroostook County townships from which the glaciers are said to have disappeared 10-11,000 years ago. Some of those men recall deliberate introductions primarily to provide a supply of bait. Records also have been found of earthworms being introduced into southwestern and western Maine by anglers. For every such instance that can now be cited there must have been very many others that never will be known. Of greater importance even than anglers have been horticulturists and floriculturists. Fruit trees early were imported to Massachusetts by Governor Endicott and to New York by Peter Stuyvesant. Apple trees and lilacs near cellar holes of so many abandoned Maine farms testify at least to a possibility of numerous introductions. When economic circumstances enabled support of floriculture locally, more or less permanent sources of earthworm dissemination were established. Worms brought from many parts of the world in soil with potted plants were protected from inclement weather in greenhouses and conservatories, permitted to multiply for several years and then were taken outside in the discarded soil. Some, however, remained in out of the way corners and under plant benches to infect the new soil that was brought in. Even today, in spite of steam sterilization, insecticides, chemical fertilizers and modern techniques, eight exotic species that have been unable to colonize outdoors linger on in the artificial habitats to which they were brought some time back, certainly in some cases more than twenty years ago. Exotics, in one greenhouse, even survived a fire that destroyed the superstructure.

Since 1935 earthworm farms may have become a much more important source of dissemination than the greenhouse industry though for fewer species. Three of the commonly cultured forms are lumbricid and can establish themselves throughout much of the United States and Canada. The fourth, which was raised for a time by a Maine dealer, is a tropical species of the African family Eudrilidae! Although purchased primarily by anglers who are likely to scatter them in all sorts of out of the way places, the earthworms are also sold to organic gardeners and farmers to improve soil fertility. The culch that is discarded from breeding beds and sold for fertilizer often contains many cocoons.

All of the forms, after expulsion from the ivied aisles of a hot-

house environment, are not able to spread uniformly in every direction. Dietary preferences now appear to be an important factor in determining horizontal distribution and they allow the fourteen Maine species to be catalogued in three groups.

1) Geophagous, including *A. chlorotica, A. longa, A. tuberculata, A. turgida, E. rosea, L. terrestris, O cyaneum* and *O. lacteum*. Of these, only *L. terrestris* copulates at the surface and though adults do seem to feed there the gut always is partly and often largely filled with earth. Kinds of soil and their pH appear to be of little significance. Each species has been found by the author in habitats with a low pH of 4.5-5.5. These worms, after omission of the little *E. rosea* and *A. chlorotica*, are just those forms used, in days before bait dealers were omnipresent, by the angler who did not have access to a manure pile and so had to get his bait in a garden. Turf, found to contain the night crawler and three species of *Allolobophora*, long has been moved about locally by man. More recently, as golf became popular and trucks common, sod has been transported to greater distances. Cocoons have been found in earth on machines that are carried about for making or modifying golf courses. Group 1 contains the species that are most widely distributed and most common in central Maine. Similar distributions are likely to have been obtained by these forms in other glaciated areas of North America.

2) Limiphagous or limicolous (mud eating or mud inhabiting), in Maine including only *E. tetraedra*, though occasional individuals of some Group 1 species appear to be at home in mud well under water or in saturated soils. In other places, *e.g.*, New York State and England, *A. chlorotica* may be limicolous at some sites. Occasional strays of *E. tetraedra* were found feeding on drier earth instead of mud. Such adaptability presumably is advantageous after introduction to a new area.

3) Litter feeding, including *E. foetida, D. octaedra, D. rubida, L. castaneus* and *L. rubellus*. Litter here is understood to include accumulations of any kind of organic matter. One of these species, *E. foetida*, doubtless originally a feeder on leaf litter was so successful in colonizing manure heaps as to be commonly known as "the" manure worm. Preference for manure has seemed so strong that in Sweden (Julin, 1949) the species is called haemerobiontic, i.e., entirely dependent on culture. However, some earthworm farmers have found that *E. foetida* does quite well in culture beds with little or no animal matter. In Himalayan hill stations to which it was introduced the species thrives wonderfully well with little if any animal food. From the manure heaps of Maine the worms and their cocoons are, of course, distributed by the farmer onto his fields and pastures at more or less regular intervals. The farmer sells other worms and cocoons to florists who put them into pots that go to many diverse

places including cemeteries on Memorial Day. The farmer also provides worms and cocoons, again of course in the manure, to town and city dwellers for indoor pots as well as outdoor flower beds and gardens. The transportation thus provided during centuries may have been of as much if not greater significance for the species than its own wandering propensity. *D. rubida* often and *D. octaedra* perhaps less frequently must have been similarly disseminated by the farmer before hay and straw as bedding were replaced by sawdust, chips, etc. A species that climbs trees (*D. rubida*) must wander and litter feeding species probably do — several specimens of *L. castaneus* and *rubellus* were seen at night away from any litter. Compost probably has been of less significance for those two species of *Lumbricus* than manure for *E. foetida* and the dendrobaenas, as in Maine people have made it for their own use. However, *L. castaneus* still was present in flower beds for a period after the compost had been applied. Individuals of geophagous species often get into organic matter and so would also be disseminated as it is used for fertilizer. This may be of more significance to *L. terrestris* as juveniles seem to aggregate in such materials. Contrariwise, litter feeders (cf. *D. rubida* above) may have to ingest considerable soil while burrowing down to unknown levels where they hibernate.

Obviously, any attempt to explain local distributions of earthworms in a glaciated area must give due consideration to the role of the only agent known to be of importance in transporting these animals.

Maine lumbricids originated somewhere in Eurasia and from a northwestern portion of that land mass and adjacent islands have been taken to every part of the world where Europeans have settled, lived or even visited. Although now common in Iceland (and also to some extent even in Greenland and Nova Zemlya), South Africa, southern South America, New Zealand and parts of Australia, permanent domicile has been acquired in the tropics (Gates, 1958) only at elevations above four or five thousand feet. One lumbricid, *Allolobophora trapezoides,* from southern Europe and supposedly common in America was not found in Maine nor is there any valid record of its presence elsewhere in New England. Some of the Maine greenhouse exotics have thriven in English artificial environments for more than a century. During that time many opportunities for outside colonization must have been provided. Yet, those same species have established themselves in southern Europe, states from Virginia south and westward, in tropical Burma, India and Malaya at elevations above 4000 feet. *P. corethrurus* originally from some equatorial portion of America is now widespread throughout the tropics but only in the lowlands. Dietary, soil and moisture preferences cannot be invoked to explain these geographical distributions. More intangible factors of the earthworm environment must be involved.

E. rosea in a breeding stage was found April 9, 1956, under a thin

layer of leaves in an exposed patch surrounded by snow and with frost still in the ground. In a little exposed ridge within a roadside ditch, thirteen active specimens of *A. tuberculata, L. castaneus, D. octaedra, D. rubida* and *L. terrestris* were taken April 7, 1956, four (of *L. castaneus, D. octaedra* and *D. rubida*) in a breeding stage. Frost still was present 2-7 inches below the surface of the ridge and snow was 2½ feet deep on either side of it. A specimen of *A. longa* with spermatophores was found on April 20, 1956, at a site where the ground was frozen half an inch below the surface. From nearby litter, with many frost crystals between the leaves, eight individuals (four with spermatophores) of the thecal morph of *D. rubida* were found. Night crawlers were seen after dark March 9, 1957, although the ground was still frozen a little below the surface. A leaf pile with considerable ice, in a lakeside woods on April 19, 1959, had many specimens of *L. terrestris* (juvenile), *E. rosea* and *A. tuberculata* (1 with spermatophores). On a little bare strip, the night of March 18, 1960, several dew-worms and a sexual adult of *L. castaneus* were moving about. Copulating pairs were seen. Snow was 16 inches deep elsewhere. Some of the crawlers were seen to emerge from beneath a thick layer of ice at bottom of an adjacent bank. Melt water from snow and ice is not too cold for many of the Maine lumbricids. Individuals secured at those early dates seemed more responsive to stimuli and to have brighter pigmentation. The brandling, usually thought to be more at home in a warm environment, not only remained vigorous while fasted for three weeks at temperatures below 5° C (Gates, MS) but also in that time regenerated normally and rapidly. In the fall, but late and after trees are bare, worms again are active. Failure of the lumbricids to colonize cultivated areas in tropical lowlands to which they were often introduced is not attributable to the vigor of any competition provided by endemics for in those same areas the equally exotic *P. corethrurus* often has become dominant.

All of which suggests that one important environmental intangible is temperature. Maine lumbricids may have become so habituated to rather low temperatures by millenia of existence just south of European ice sheets as to be unable to perpetuate the species in more equable climates. Certainly in Maine, even for part of the *E. foetida* population, hibernation is required by the climate. Nothing is known about the state in which the winter is spent. Aggregation in balls of dozens to hundreds of individuals has been maintained by laymen, but the author has yet to find some one who had seen such clusters or who had witnessed their exhumation. Duration of winter rest of course varies from one year to another as the ground may freeze early in November or not until late in December. Furthermore, emergence to the surface or return to an active stage may become possible early in March or not until late in April.

Estivation also seems to be imposed, for most individuals of geophagous species, by the Maine climate. This time of rest also is

of variable onset and duration. In a dry spring, worms become hard to find in open areas even in May. Ususally summer quiescence is continued through September well into October. Thus, for several species there usually are two periods of activity as well as of breeding in a calendar year. There is, however, a possibility that an unusually cool and wet summer can obviate quiescence or that a dry fall and early freezing can prevent autumnal activity and breeding.

The Maine climate is of the humid continental sort and in the most thoroughly studied section the average annual rainfall is about 40 inches with monthly averages of 3-4 inches. Four inches, in spring and fall, then provides sufficient moisture to enable activity but not in summer months. Only 2.65 inches during October-November is sufficient to permit considerable activity in Allahabad but in Rangoon and Akyab 9 and 16 inches respectively, during those same months, is not enough. In Burma, increasing hours of bright sunshine and hardening of the top soil is associated with decreased activity. In Maine summers the top soil of open areas also hardens.

Reproduction in each species of *Lumbricus* and *Allolobophora* as well as for *Eisenia foetida* is biparental. Parthenogenesis is obligatory, in Maine, for *D. octaedra, E. rosea, O. cyaneum, O. lacteum* and probably also for *E. tetraedra.* In *D rubida,* uniparental reproduction is of course obligatory for male sterile morphs that are rare and obtainable in but small samples. The thecal morph which was found more often and in larger numbers appears to reproduce sexually. As *E. rosea* is the only really common uniparental form, parthenogenesis and any associated polyploidy has not usually proved to be of such great advantage after introduction, at least in Maine, as has sometimes been thought. Similar findings now are anticipated in other glaciated areas of North America. Not always appreciated in this connection is the fact that a single *ex copula* individual can lay for several weeks and that in some species two or more young may emerge from each cocoon.

Most earthworms, from the dwarf species that are about one millimeter thick to the giants that may be 25 mm thick and six or more feet long, have no special respiratory organs. The skin, accordingly, must always be moist enough to permit respiration. But drouth comes sooner or later in the life history, and perhaps even in the humid tropics, to all earthworms except those living in or able to take refuge in permanently wet sites. Some evidence already is available to show that embryonic development of several species (cf. for instance, Murchie, 1960, p. 205) can be interrupted because of insufficient moisture without deterimental results. A similar capacity seems to be necessary in the monsoon tropics and may well prove to be common in megadrilous oligochaetes when this matter is studied. After hatching, lethal effects of drouth are avoided only by cessation of normal activities. This period of inactivity is passed in a state herein called diapause about which a little information has been recorded or in other states about which nothing is known.

Inactivity also is imposed in northerly portions of the temperate zone during some portion of the winter, but nothing is known about the state in which this period is passed although the literature provides some evidence that several lumbricids are able to survive freezing. These alternations of reduced metabolism and gross or macroscopically recognizable activity occur once a year in monsoon lands and twice a year in Maine. Such recurrences constitute a kind of periodicity but without the calendar precision that dictionary definitions seem to require. In earthworms, the phenomenon because of its association with climatic conditions can have no more regularity than does the weather.

Although such periodicity has for many millenia been forced upon the lumbricids now domiciled in Maine, ten of them (in appropriate conditions) still can remain active throughout the year. Three other species, with data lacking only for several months, probably have retained a similar capacity. The fourteenth lumbricid, *E. tetraedra* (as well as three other Maine species, *E. foetida, E. rosea, D. rubida*), was found (Omodeo, 1948) in an unspecified section of Italy to be breeding throughout the year. *A. trapezoides,* probably widely distributed in warmer portions of the United States, according to the same author also breeds the year round. *B. parvus,* as indicated by data secured in the Orient, probably also is similarly characterized. Those sixteen lumbricids are the species that have colonized most widely in overseas areas to which European earthworms were transported by man.

Most of the geophagous species that remain active throughout much or all of the year in northern India and in Burma are of foreign origin. Geophagous endemics, in the same areas and with few exceptions, seem to be unable to take advantage of artificially supplied moisture during climatically dry periods.

The basic facts of earthworm periodicity long have been known to jungle dwellers in the orient and to laymen in the occident but more especially perhaps to anglers. However, authors of angling classics, from the anonymous predecessor of the prioress Juliana de Berners to Izaak Walton, who long ago probably could have supplied important information, were more interested in writing about fish and fishing than in recording their observations on earthworms. Few biologists have investigated earthworm ecology in the field and from laboratory data, at least in the case of *A. longa,* were derived erroneous conclusions. Paucity of earthworms, present only in two of several hundred soil samples from the Woods Hole portion of Cape Cod, was attributed (Philips, 1923) to low soil pH. Yet, even during the dry summer months when those observations were being made, lay employees of the Marine Biological Laboratory Supply Department were collecting dew worms and were also able to supply live brandlings. The laboratory derived conclusions (Arrhenius, 1921) that Philips cited were also invalid and pH, at least in most soils,

is now known to be of little importance to various geophagous earthworms. Humus and litter also seem to be of little importance to many species. Tropical soils, for instance, are said to be poor in organic matter yet they support large earthworm populations. Furthermore, at depths where even less organic matter is to be expected, giant species are common not only in Burma but also in India and Ceylon.

Many of the Maine lumbricids (all but five) were for a time included in *Helodrilus*. The genus, *sensu stricto,* never has been found outside Europe and the name in its broad and actually supergeneric sense was abandoned more than thirty years ago by taxonomists. Usage of *Helodrilus,* as a habitat designation in American literature, also was incorrect because of intrageneric variation in dietary preference. Intraspecific variation likewise requires caution or qualification in physiological as well as morphological generalization about earthworms. Texts often convey the impression that these animals drag leaves and other materials into burrows or feed and copulate on the surface. In Maine only night crawlers have been found to engage in such activities. Nevertheless, in some northern states occasional individuals (presumably "jacked" at night while feeding on the surface) of another lumbricid were sold by supply houses as *terrestris* (Gates, MS) with the result that impossible anatomical variation has been recorded for the latter species. Copulation, in the literature, always is between clitellate individuals but aclitellate specimens with no signs of postsexual regression occasionally were found on dissection to have their spermathecae fully charged with male gametes. Worms taken in copula have proved, again on dissection, to be male sterile and incapable of exchanging sperm. Spermatophores without sperm have been seen on male sterile worms and spermatophores with sperm on individuals of parthenogenetic morphs that had lost all organs for storage of male gametes. Clitellate and seemingly mature specimens of taxa with obligatory biparental reproduction sometimes have empty spermathecae, naked male gonoducal funnels and no eggs in the ovaries. One Maine lumbricid, *E. tetraedra,* that is said to breed year round in Italy, appears to estivate, according to hitherto available data, in Maine even when the site is saturated. The green variety of the geophagous *A. chlorotica* lives under permanent water at several sites and the red variety is known in the States only from manure. As already noted above, the limicolous *E. tetraedra* was found in unsaturated soils and individuals of geophagous species were found in litter and in mud where they did not have to estivate as would have been necessary in their usual habitat. Such instances and others of a similar sort that can be cited suggest a need for caution in accepting generalizations based on a few laboratory experiments or short studies in limited areas.

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A Population Study of the Gray Fox[1]

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ABSTRACT: An attempt was made to analyze some of the component forces of some gray fox populations in northern Florida. The size of the populations studied was determined by the use of an age-ratio-reduction method. In this method the size of the population was indirectly derived by determining the magnitude of the effect on the age ratio of sterilizing a known number of females. A knowledge of the degree of reduction of the age ratio caused by sterilizing these females allowed the calculation of the entire female population. Application of the sex ratio permitted an estimation of the size of the entire fox population.

It was possible to estimate the size of these same populations by several variations of the recapture method (Lincoln Index and Schnabel method) and the removal method. The recapture methods usually gave higher estimates than the age-ratio-reduction method. The estimates of the age-ratio-reduction method indicated a density of slightly less than 3 to 4 foxes per square mile.

From recapture distances, a probable approximate diameter of two miles was estimated for the size of the home range of the gray fox in this region. Groups of foxes of family composition were captured in areas isolated from captures of other foxes and were termed family aggregations. Twenty-one family aggregations were found. The diameters of these family aggregations were in close agreement with the recapture data concerning the estimate of the size of the home range.

This study explores the possibility of estimating the size of a gray fox (*Urocyon cinereoargenteus floridanus*) population by altering the breeding capacity of a known number of females and determining the effect on the age ratio of the population. The size of the population is deduced from the magnitude of this effect. The study also includes investigations of reproduction, mortality, and movement.

The census method is similar to the methods used by Allen (1942), Kelker (1940;1945), and Riordan (1948) in estimating the sizes of populations of game animals that were selectively hunted according to sex. Their method was to compare pre- and post- open season sex ratios after which they computed the size of the populations by the use of knowledge of the number of male and/or female animals killed. Kelker's formulae estimated population sizes for each sex and fawns separately. The age ratio was used to determine the number of fawns, but the observed change takes place in the adults rather than in the young as in the method presented here.

The recapture method (Jackson, 1939) derives an estimate from the proportion of marked individuals in the population. In contrast to the recapture method, the age-ratio-reduction method presented here does not require the recapture of a large number of the pre-

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viously trapped animals. The capture and sterilization of a single female reduces the number of juveniles in the coming year's population by nearly five, a large change for a small effort. Foxes are difficult animals to trap and possess considerable ability in learning to avoid traps. This makes the age-ratio-reduction method more useful than the recapture method.

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PROCEDURE AND METHODS

In brief the procedure was to catch foxes on an area before the breeding season, mark them, and release them. The females were sterilized by surgical hysterectomy. The juvenile-adult ratio was noted. The purpose of marking was to prevent counting an animal twice. A year later a sample was obtained from the population, duplicating as nearly as possible the trapping effort of the first year. The juvenile-adult ratio was again noted. It was assumed that the decline in the ratio of juveniles to adults was related to the number of females sterilized. The total females in the population were estimated by calculating the number of females required to be sterilized to produce a complete decline in the juvenile ratio to zero. By applying the sex ratio the entire population was determined.

Certain assumptions are made in the age-ratio-reduction method used in this study: (1) the sterilization is complete; (2) the sex and age ratios in the sample are representative of the actual sex and age ratios of the population; (3) there is no immigration or emigration of foxes from the area; (4) the reproductive rate and probability of dying remain constant during the study or changes can be determined and adjusted for; (5) there is no loss of marks on the foxes for the first year; (6) the relative trapability of young and adults does not change during the time of the study; (7) there is no marked change in the behavior of the sterilized females; (8) no other factor, such as climate, changes enough during the time of

the study to affect the age ratio; and (9) the observed reduction in the ratio of juveniles to adults from the first year to the second year was due to the sterilization of the female foxes.

The following efforts were made to check the above numbered assumptions: (1) penned females and recaptured females were examined after a lapse of time; (2) the sex and age ratios were compared with each other and with other populations of foxes from this region (Wood, 1959); (3) a mile wide peripheral area was set up around each experimental area to determine the extent of movement of the foxes, also the region for about 15 miles around the plantation areas was trapped and any massive emigration from the study areas would have shown up in the capture of tagged foxes outside of the study areas, existing natural barriers restricted movement on a third study area; (4) an examination of the age classes of the population and the mortality rates for both years indicated the constancy of reproduction and mortality; (5) the use of the ear tattoo ruled out loss of marking of the foxes; (6) the extent of trap avoidance was determined to a degree by comparing recapture rates of different classes of adults; (7) a number of penned, sterilized females were kept under observation to determine if any marked change in behavior occurred; and (8) an examination of the Weather Bureau data gave a check on the stability of the weather during the two years. These checks are not absolute tests of the degree to which any of the assumptions varied from the expected, however, they were sufficient to detect any serious deviation.

A central area, six square miles in size, was set up for the area wherein the female foxes were to be surgically treated. This area coupled with a one mile wide peripheral area, selected on the basis of the size of the home range (Sheldon, 1950;1953), there resulted a total of 20 square miles for each study area. Two experimental and one reference (control) areas were established.

The size and compactness of the areas required, limited the choice to the Norias and Sunnyhill plantations located between Thomasville, Georgia and Tallahassee, Florida. The Panacea unit of the St. Marks National Wildlife Refuge was chosen for the third study area, because of its apparently high fox population. Boundary difficulties restricted the placement of the study areas on the plantations, resulting in the southern quarter of these two areas having a common peripheral area one and a half miles wide. A large wedge of land lay between the northern ends of these areas, which, although outside the agreed peripheral areas, was also trapped because of its location (Fig. 3). Lake Miccosukee was used in locating the central area on the Norias plantation. However, at the beginning of the study the lake went dry. The lake bed was examined on several occasions and the tracks indicated that few foxes ventured far out. Placement of the study area on the Norias plantation resulted in approximately 20 square miles being trapped and 18 square miles being trapped on the Sunnyhill plantation. The natural barriers

around the Panacea area resulted in only 16 square miles being trapped.

Aerial photographs, obtained from the United States Department of Agriculture, were used to prepare maps of all three areas and to locate all the small roads that were to be trapped. A 0.1 mile grid was placed permanently on the map and cross referenced. The location of every animal trapped was obtained by this cross-reference system to the nearest 0.05 miles.

The trap used to catch the foxes was the Victor Number 2, coil spring, square jaw fox trap, manufactured by the Animal Trap Company of America, Lititz, Pennsylvania. Attempts to prevent injury by steel traps were made by wrapping the jaws in various ways; all proved unsatisfactory. Damage to the leg or foot of the animal was found to be due to escape efforts. To prevent this type of injury, all traps were fastened to a light drag, which would allow the animal to leave the point of capture, but seriously impede progress. A dog, a Golden Retriever, was used to track these animals, which he did with great skill after once learning the procedure. The use of this dog increased the efficiency of the trapping by an estimated thirty per cent.

The set used in trapping was described by Wood (1954). Seventy to one hundred and twenty traps was the usual number of traps in operation. The distance between traps varied slightly, but generally was 0.1 miles. When a road was retrapped, the traps were usually placed at different spots. Traps were run every day and usually left in the ground for seven days. During the hottest weather, scent was applied twice during the week after the initial setting because of excessive evaporation. After every rain, traps were both rescented and reset. By alternating the trapping weeks on the three different areas, a relatively equal trapping effort was made on each area. Trapping was stopped on the Sunnyhill plantation on October 18 and on the Norias plantation on November 18, to allow for dog training prior to quail season. On the Panacea area, trapping was continued until December 18 in 1954 and December 24 in 1955. Trapping began June 14 the first year and June 13 the second year.

The method of altering the age ratio of the population was that of surgical sterilization of the female foxes. The surgical technique followed was similar to the veterinary "spaying" of female dogs, except that in this study only a portion of each uterine horn was removed. Thus the ovaries and portions of the uterus were left intact. It was hoped that this procedure would prevent an alteration in behavior and activities due to endocrine changes. The wound was then sprinkled with Terramycin and coated with collodion to keep screw worm fly larvae out of the wound. The nocturnal habits of the fox were probably more effective than anything in avoiding this hazard. Each fox was given 1 cc (300,000 units) of procaine penicillin in sesame oil intramuscularly. A simple laparotomy was per-

formed on the female foxes from the reference area (Sunnyhill plantation).

The operation on the foxes caught on the plantations was performed in a laboratory in Thomasville, Georgia, on the same day that the fox was caught. Foxes were brought into the laboratory in a burlap sack, through which Nembutal was administered intraperitoneally. After the operation the foxes were placed in small cages to recover from the anesthetic and were released early the following day at the point where they had been captured. The operation on the foxes from the Panacea area was performed in the back of a bakery delivery truck converted for use in running the trap lines.

A method for determining the age of wild foxes was developed by Wood (1958). This method used the constant wear on the molars and the fact that foxes are all born within a short period of time in early spring. Thus foxes caught at any time of the year can be aged with a reasonable degree of accuracy to the month, on the assumption that all foxes are born in March.

In addition to the tooth wear method, the weight of a fox from June until the middle of August will clearly separate the adult foxes from the juveniles, but in the middle of August some juveniles begin approaching six pounds, the minimum weight of some adults. Most female foxes with small mammary nipples are juveniles and those with large nipples are undoubtedly adults. Juvenile foxes have characteristically puppy fur up until about the middle of August. In late summer, when juveniles are approaching adult size, young foxes may be distinguished at a distance by their brightly colored bushy tails. The tail of adults at this season is faded and badly worn, showing a shedding of hair prior to the growth of new hair in fall. In addition to all these factors, it is possible for a worker handling many foxes to know by other, particularly facial, characteristics the difference between young and adult foxes (Fig. 1).

The following data were recorded from all trapped foxes; date of capture, location of capture, sex, age, weight, size of mammae, and presence or absence of milk. At the time of hysterectomy, the number of placental scars was recorded. During the first year of the study all animals were marked with small aluminum ear tags posessing a number and a return address. About half way through the first year foxes also received a number tattooed into their ear. During the second year all of the animals caught were killed.

DESCRIPTION OF AREAS

The Panacea area is typical of the coastal strip in this region. Since the area is only one mile from the Ochlochnee Bay, the land rises only a few feet above sea level. It is a low rolling sandy region with lime sink ponds of various sizes and slow flowing streams. There is one large lime sink on the area called Otter Lake, a permanent cypress lake. The remainder of the lime sink ponds are not very deep and are inclined toward rapid plant succession. Buckhorn Creek,

a tributary of the Ochlochnee River, bounds the western end of this study area. To the west of this creek are reed-covered mud flats cut by several channels of the Sopchoppy and Ochlochnee Rivers, an effective barrier for foxes. To the east of the area lies Oyster Bay and to the south lies Ochlochnee Bay, both are also effective barriers. Any large amount of movement of foxes to or from the area must occur to the north. Within the fenced area of the refuge are

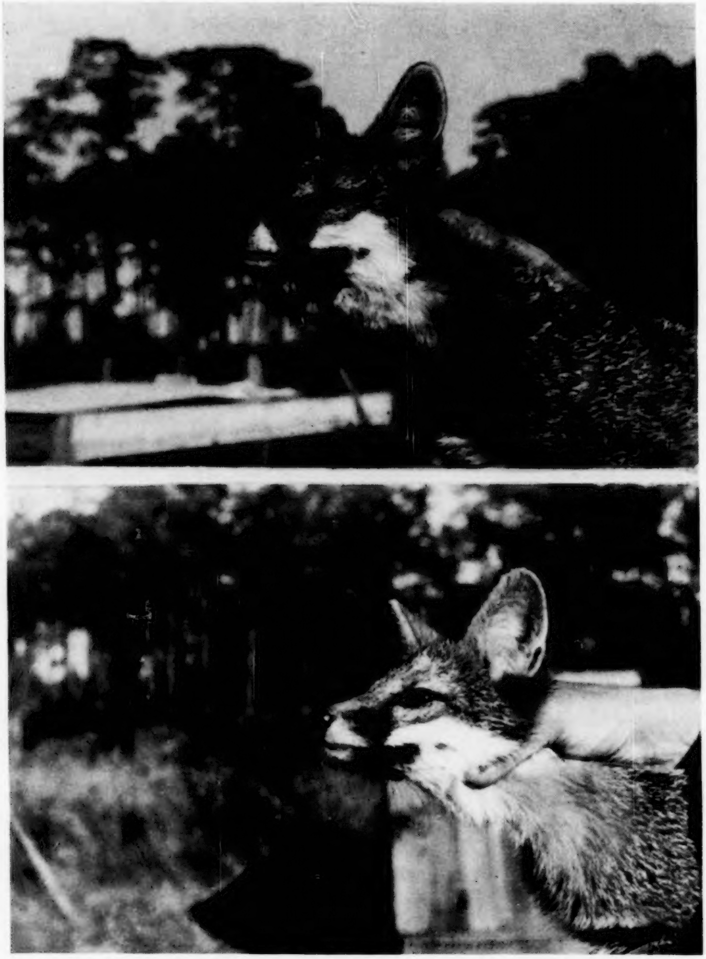

Fig. 1.—Facial characteristics of adult (above) and juvenile (below) gray foxes.

two large, formerly paved roads, numerous small sandy roads, section line clearings, and fire lanes resulting in unusual accessibility to every part of the study area.

The Norias and Sunnyhill Plantations are typical of the steeply rolling land of the Tallahassee red hills. They lie about 200 feet above sea level. Both areas have lime sinks but in contrast to the Panacea area, most of these were dry. No permanent streams flow on either area and the drainage pattern is erratic. The Norias Plantation sits on the northern end of Lake Miccosukee which is about 15 miles long and averages about a mile in width. Both plantations are surrounded by other smaller plantations and both have several unpaved county roads passing through them. Besides these roads many private agricultural roads cut between the fields. It was these agricultural roads that were used as trap lines for this study. The management of the plantations has a dual purpose, diversified farming and game management. The principle game species are the bobwhite quail and wild turkey. Corn is the main crop planted on both plantations.

TABLE I.—Trapping results

	Panacea		Norias		Sunnyhill	
	1954	1955	1954	1955	1954	1955
Total Foxes	60	29	63	38	31	45
Adults	22	15	24	17	12	13
Juveniles	38	14	39	21	19	32
Total Male Foxes	30	14	31	20	16	27
Adults	11	9	13	12	6	8
Juveniles	19	5	18	8	10	19
Total Female Foxes	30	15	32	18	15	18
Adults	11	6	11	5	6	5
Juveniles	19	9	21	13	9	13
Sterilized Females Released	13	..	14	..	7*	..
Adults	6	..	5	..	3	..
Juveniles	7	..	9	..	4	..
Foxes Accidentally Killed	8	..	7	..	0	..
Males	3	..	2	..	0	..
Females	5	..	5	..	0	..
Foxes Released	54	..	56	..	31	..
Males	27	..	29	..	16	..
Females	27	..	27	..	15	..
Foxes Recaptured	15	7	7	7	5	2
Males	5	3	4	3	1	0
Females (intact and sterile)	10	4	3	4	4	2
Sterile Females	5	3	1	1	1	0
Foxes Re-released	13	..	7	..	5	..
Placental Scars	2,3,4,5	3,3	4,5,6,6	4,4,4	..	4,5,5
Trap Nights	3,038	3,182	4,435	4,744	2,387	3,475
Foxes Per Trap Night	.0197	.0091	.0142	.0080	.0129	.0129

* Laparotomy.

Prior to this study there had been essentially no trapping on the Panacea area since the incorporation of this area into the St. Marks National Wildlife Refuge in 1936. Trapping on the plantations prior to the advent of the fox investigations in 1952 was confined mainly to the tenant farmers and one of the supervisors who trapped for a bounty paid by the plantations. Before the beginning of this study 50 foxes were trapped by J. E. Wood in 1953 on the Norias Plantation and 24 were trapped on the Sunnyhill Plantation in the early spring of 1954.

RESULTS

The numerical results of the trapping are listed in Table I. There was an indication of trap avoidance by the male foxes. Since this avoidance factor was only one of the possible reasons for the difference between recapture rates of intact females and males (for instance, the difference might possibly have been due to excess mortality or emigration of males), the factor was called "absence of males" in the analysis of the data. The data also gave indications of the extent of the mortality of the female foxes due to the sterilization operation.

In an effort to determine the extent of mortality of the sterilized females and as a practice in developing the surgical technique, eight female foxes (from other areas) were hysterectomized. These eight foxes were then retained in cages to determine the outcome of the operation. All of these foxes survived. In February, eight months after the operation, these foxes were again opened up, their ovaries removed, and the success of the hysterectomy determined; the uterine horns were well healed and discontinuous. None of these foxes could have been successfully fertilized.

On September 4, 1954, an adult, apparently female fox weighing 11 pounds was caught in the central area of the Norias Plantation. According to the tooth wear, this fox was 17 months old. When the hysterectomy was performed, the fox was discovered to be a probable transverse hermaphrodite with underdeveloped, undescended testes. Because this fox was not a part of the breeding population of the Norias Plantation it was not used in the calculation of the population by the age-ratio-reduction method.

ANALYSIS OF DATA

Panacea Area

The number of foxes present on the Panacea area in 1954 has been calculated from the data in Tables I, II, and IV. The formula derived declares that:

$$\frac{\text{number of females sterilized}}{\text{reduction in the age ratio from the first to the second observation}} : \frac{\text{(X) the total females in the population}}{\text{a total reduction of the age ratio to zero}}$$

These calculations give an estimate of 66 foxes. The following outline gives the steps for this estimate.

A. *Basic Information.*—In 1954 there were 38 juvenile and 22 adult foxes captured; giving a ratio of 1.73 juveniles to every adult. Eighteen of these foxes were females that were fixed (sterile or dead). In 1955, 14 juvenile and 15 adult foxes were captured; a reduction in the age ratio to 0.94 juveniles to each adult.

B. *Calculations:*

1. a change from 1.73 to 0.94 was a reduction of 0.79
2. $$\frac{18}{0.79} : \frac{X}{1.73}$$
3. X = 39 female foxes
4. 2X = 78 foxes in 1954

or 1955 adjusted for absence of adults:

$$\frac{14 \text{ juveniles}}{18 \text{ adults}} = \text{ratio of } 0.78$$

then

1. a reduction of 0.95
2. $$\frac{18}{0.95} : \frac{X}{1.73}$$
3. X = 33 female foxes
4. 2X = 66 foxes in 1954

In explanation of the above outline, the 5 dead females (accidental deaths from various causes, Table I) were included in the fixed female category because they too, were removed from breeding. The adjustment for the absence of adults is made because it was noted that a recapture rate of 19 per cent (all areas combined, Table II) was made for the intact (unsterilized females, but the recapture rate for the treated females was only 13 per cent (Table II). This difference was attributed to some effect of the surgical operation. However, the death or absence of these females did not affect their influence in changing the age ratio of the population, but it did have an effect on the number of adults expected to be captured in 1955. The 10 per cept recapture rate of male foxes also affected the number of adults captured in 1955. The difference in the males was attributed to either trap avoidance, or mortality, or both. Therefore a sufficient number of adult foxes were hypothetically added to the 1955 data to bring the total up to the 19 per cent recapture rate of the intact females. This amounted to 3 foxes for the

Panacea area and resulted in a difference of 12 foxes between the unadjusted and the adjusted population estimates. The intact females must also have experienced some mortality and learned to avoid traps to a degree. Thus, these adjustments are minimum ones for disturbances wrought by the trapping procedure and must have exceeded the three foxes added.

The recapture method may be compared with the age-ratio-reduction method as follows:

1954, released 52 marked foxes

1955, 15 adult foxes were caught, 7 of these were recaptures

$$\frac{7}{15} : \frac{52}{N}$$

$$N = 111 \text{ foxes in 1954 (unadjusted)}$$

However, this figure is still unadjusted for the absence of some adults as described in the previous method. To adjust for these adults in this method, it is assumed that these adults were marked

TABLE II.—Release and recapture results of gray foxes within 1954

	Males		Intact females		Sterilized females	
	Re-leased	Recap-tured	Re-leased	Recap-tured	Re-leased	Recap-tured
Panacea	27	5	15	5	10	5
Norias	30	4	16	2	13	1
Sunnyhill	15	1	11	4	4*	1
Total	72	10	42	11	27	7
Per Cent Recaptured	13.9		26.2		25.9	

* Laparotomy

1954 to 1955

	Males		Intact females		Sterilized females	
	Re-leased	Recap-tured	Re-leased	Recap-tured	Re-leased	Recap-tured
Panacea	27	3	13	1	12	3
Norias	30	4	15	4	14	1
Sunnyhill	15	0	9	2	6*	0
Total	72	7	37	7	32	4
Per Cent Recaptured	9.7		18.9		12.5	

* Laparotomy

animals (otherwise their absence would have been undetectable).

Thus, hypothetically:

1955, 18 adult foxes were caught, 10 of these were recaptures

$$\frac{10}{18} : \frac{52}{N}$$

N = 94 adult foxes in 1954 (adjusted)

The Schnabel (1938) method, a refinement of the recapture method adapted to continuous trapping over a period of time, may be applied to the data from the Panacea area. In this case the Schnabel method is not a refinement of the recapture method already presented, because that method was concerned with recaptures from 1954 to 1955. The Schnabel method which follows for the Panacea data is concerned only with releases and recaptures within 1954, and the results are therefore independent of the recapture method already described.

Schnabel Method:

Time Period	Number Caught A	Marked Caught C	Marked at large: Unadjusted for Mortality B	Marked at large: Adjusted for Mortality D	AB	AD
Aug. 17-24	35	0	0	0	0	0
Sept. 20-25	6	3	35	33	210	198
Nov. 22-30	19	6	41	35	780	665
Dec. 1-18	11	4	60	54	660	595
Totals		13			1650	1458

$$N = \frac{\Sigma(AB)}{\Sigma C} = \frac{1650}{13}$$

N = 127 foxes in 1954 (unadjusted)

or

$$N = \frac{\Sigma(AD)}{\Sigma C} = \frac{1458}{13}$$

N = 112 foxes in 1954 (adjusted for mortality during trapping)

Column D in the method shows the adjustment for mortality of the marked foxes during the trapping. The adjustment made was based on the assumed constant 0.64 annual probability of dying (Table III).

It is also possible to adjust this method for the absence of some foxes due probably to trap avoidance. However, the recapture rate applied is that for 1954 intact females which was 26 per cent as opposed to the 19 per cent recapture rate of intact female foxes a year later (Table II). The resulting three extra foxes were added to the last line of the captures in the outline of the method. The adjusted results are as follows:

$$N = \frac{\Sigma(AB)}{\Sigma C} = \frac{1830}{16}$$

N = 114 foxes (adjusted for trap avoidance only)

The combined adjustment for trap avoidance and mortality during the trapping gave an estimate of 101 foxes for the Panacea area in 1954.

On this area, due to the large capture of foxes (37) the first week of trapping in 1954, it was possible to apply the recapture method in three different ways. The number of captured and released foxes

TABLE III.—Age groups and mortality of the gray fox

	Number of foxes		Annual probability of dying		
Age	1954	1955	Within 1954[1]	1954-55[2]	Within 1955
Panacea Area					
7 months	38	14	.63	.66	..[3]
19 months	14	13	.64	.78	.77
31 months	5	3	.60	1.00	1.00
43 or more months	2	0	1.00	1.00	..
Norias Plantation					
7 months	39	21	.69	.69	..[3]
19 months	12	12	.43	.75	.75
31 months	7	3	.71	.71	.33
43 months	2	2	0.00	1.00	1.00
55 or more months	2	0	1.00	1.00	..
Sunnyhill Plantation					
7 months	19	31	.63	.63	.72
19 months	7	7	.57	.71	.71
31 months	3	2	.33	0.00	0.00
43 or more months	2	3	1.00	1.00	1.00

[1] This probability of dying is calculated from the difference in size of of the age classes in 1954. It assumes that birth and death rates were constant for each age class for 1951, 1952, 1953, and 1954.

[2] This probability of dying is calculated from the difference in size of a group of siblings from 1954 to 1955. It assumes that the same proportion of the total population was caught both years.

[3] This figure was not entered because it was altered from the normal by the sterilization of female foxes in 1954.

of the first week was compared with the number of captures and recaptures of the 2nd week, the 3rd week, and the 2nd and 3rd weeks combined. If the comparison is made with the 2nd week, the population estimate is 66 foxes in 1954. If the comparison is made with the 3rd week, the estimate is 104 foxes, and if the comparison is made with both weeks combined, the estimate is 92 foxes.

The removal method can be applied to the Panacea data because of the large catch made on the initial week of trapping. For data of this type the number of trappable foxes in 1954 may be visually estimated at about 70 (Fig. 2).

Norias Plantation

The population estimate of the Norias Plantation by the age-ratio-reduction method was 62 foxes for 1954. The adjustment for the absence of adults amounted to only 2 foxes. An adjustment for an increase in young was made, based on the fact that the reference

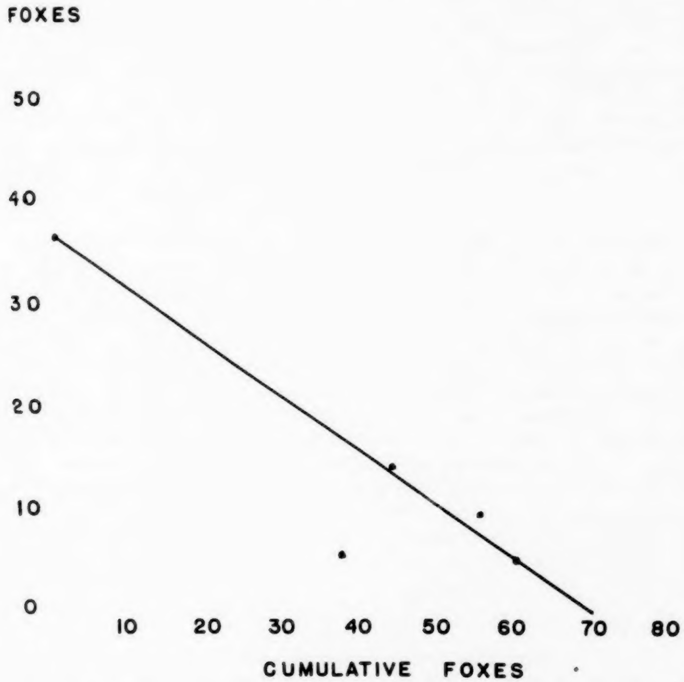

Fig. 2.—The removal method of estimate of population at Panacea. The ordinate gives the weekly catch of foxes. The abscissa gives the cumulative total.

area, the Sunnyhill Plantation, experienced a 0.40 increase in young (adjusted for trap avoidance) in 1955 over the 1954 figure. Since this area is adjacent to the Norias Plantation and the proportion of juveniles was nearly the same for both areas in 1954 (61% Sunnyhill and 63% Norias), it was felt necessary to apply this increase to the Norias population (see assumption 4).

By the recapture method, the unadjusted estimate was 136 foxes on the Norias area in 1954. When adjusted for the absence of adults, the estimate was 118 foxes.

The estimate obtained by the Schnabel method was 161 foxes, or 155 foxes when adjusted for mortality during trapping. When adjusted for the absence of adults, the estimate was 118 foxes, and with both of the above adjustments combined, the estimate was 100 foxes for the Norias area in 1954 by the Schnabel method.

Sunnyhill Plantation

Because the Sunnyhill Plantation served as the reference area for the study, there can be no calculations of the population by the age-ratio-reduction method. However, the recapture method gave an estimate of 202 foxes (unadjusted), or 99 foxes when adjusted for the absence of adults. According to the Schnabel method, the estimate was 75 foxes (unadjusted), or 71 foxes when adjusted for mortality during trapping, or 56 foxes when adjusted for trap avoidance. The combined adjustments for the Schnabel method estimated 54 foxes on the Sunnyhill area for 1954.

DISCUSSION

Panacea Area

The estimates of the various methods for determining the size of the same population ranged from 66 to 127 foxes. Many of the observed differences were probably due to trap avoidance (which could not be completely adjusted for) on the part of the foxes. Because it is more greatly affected by this factor, the recapture method gave consistently higher estimates than did the age-ratio-reduction method. The removal method gave essentially the same answer as the age-ratio-reduction method, indicating that in 1954, nearly all of the foxes were trappable on the Panacea area. Using the age-ratio-reduction method, the density of the foxes was about 4 per square mile. Conceivably, the area influenced by the trapping was greater than the 16 square miles trapped. Foxes that have an average home range diameter of about 2 miles, would be expected to range into the study area from outside.

Norias Plantation

On the Norias Plantation the recapture method again gave an estimate higher than that of the age-ratio-reduction method. The removal method and the recapture method applied within 1954 on the Panacea area, were not usable for the Norias area because there was no large initial catch of foxes during the first week of trapping.

The previous trapping experience of the foxes on the plantation areas probably accounts for their wariness as compared with the fox population on the Panacea Unit of the St. Marks National Wildlife Refuge. On the basis of 62 foxes estimated for the Norias area by the age-ratio-reduction method, the density of foxes was about 3 per square mile.

Sunnyhill Plantation

The fox population on the Sunnyhill area was expected to be nearly the same as that on the Norias Plantation. Yet the estimates for the Sunnyhill Plantation were considerably lower (comparing the same methods) than those for the Norias Plantation. The difference in size of these populations may be readily explained by the fact that 24 foxes were removed from the Sunnyhill area in March and April of 1954 by J. E. Wood for another phase of the over-all fox study (Wood; 1954, 1955, 1958, 1959). If these foxes and their expected progeny, minus a mortality of 0.30 for one half a year, were still at large on the plantation when the study commenced in June of 1954, they would add 44 foxes to the population bringing it up to a figure comparable to the estimates made for the Norias Plantation by the recapture method.

DISCUSSION OF ASSUMPTIONS

Having arrived at estimates for the sizes of the populations, it becomes desirable to examine the assumptions made in these methods in the light of the efforts made to check them.

(1) The sterilization is complete.

This assumption is probably entirely correct because every one of the 8 caged animals and all 11 of the recaptured females that had been sterilized showed complete and apparently permanent separation of the reproductive tract.

(2) The sex and age ratios in the sample are representative of the actual sex and age ratios.

This assumption is probably nearly correct since ratios obtained by Wood (1954, 1955, 1958, 1959) in the same region compare favorably with those obtained by this study. In support of the surmise that there is no tendency for one of the age or sex classifications to be caught more easily than others, is the observation that the sex ratios in all cases (except the reference area in 1955) are very close to the expected 50-50 ratio and the age groups are likewise close to the expected values. The juvenile ratio never exceeded the average number of young as determined from the reproductive tracts (Wood, 1955).

(3) There is no immigration or emigration of foxes to or from the study areas.

The mile wide peripheral area around the 6 square mile central area wherein the females were sterilized was designed to check this assumption. Also natural barriers of water were used whenever possible to minimize movement. As a further check on the movement of foxes out of the areas, other members of the over-all fox study trapped the

smaller plantations around the Norias and Sunnyhill plantations for a distance of 15 miles. The tags in the foxes' ears contained a return address to further aid the possibility of recovery. The recaptures indicated that the average home range of the gray fox in this region was probably about 2 miles in diameter or a little more than 3 square miles in area.

In reference to emigration, two foxes were recaptured outside the study areas. One of these was caught 11 miles from its first capture. The other fox was caught three and three-quarters miles from its first capture, but only one-quarter mile from the outside boundary of the peripheral area. There was no check on the immigration other than that from the peripheral to the central area. Only one fox shifted in this direction while 3 shifted from the central to the peripheral area. Most of the shifting of ranges occurred between December and March. The following discussion of assumption 4 indicates that some movement probably did occur on the Norias Plantation (and if so, probably on the Panacea area too, but to a lesser degree because of natural barriers). However, the analysis of the data does not produce an unreasonably high estimate (which it would if many of the sterile females emigrated) and thus most of this movement probably occurred between the peripheral area and the surrounding relatively lightly trapped region. These females would then have had an effect on the lowered juvenile ratio of the study area due simply to their proximity. Movement apparently did not seriously affect the results of the method.

(4) That the reproductive rate and the probability of dying remain constant during the study.

There was no way to check directly the mortality of the foxes. There was indication that at least on the reference area, either the reproductive rate jumped above the average for the region (4.48) to 6.40 young per female, or the trap avoidance by the adults caused this apparent increase. The recapture rate in the reference area the second year was remarkably low (Table II). However, even when the data were adjusted for trap avoidance as previously discussed, there was still an increase of 0.4 juveniles per adult on this area due either to increased reproduction or trap avoidance of adults. The adjustment made for this factor in calculating the size of the Norias fox population was labeled "increase in young," to distinguish it from the previous adjustment for trap avoidance. Perhaps, if the reproductive rate was stable, this adjustment was then an additional check on trap avoidance which may have accounted for all trap avoidance. However, when this factor ("increase in young") was introduced into the calculations of the size of the Norias fox population, the resultant answer indicated that all foxes were caught in 1954. If all foxes were caught in 1954, and no movement occurred into the area, then all adults captured in 1955 should have been marked (providing there was no loss of ear tags). But there were ten unmarked adults captured on the Norias Plantation in 1955. Although there was no loss

of marking within the first year, there was a 33 per cent loss of ear tags in these foxes from 1954 to 1955 (Lord, 1956). This could account for five or six of the unmarked foxes, but the remaining four or five unmarked adult foxes must either have avoided the traps in 1954 or moved into the area during the nontrapping interim between 1954 and 1955. If the former was the case, then providing for mortality, 14 foxes were left untrapped in 1954. But the adjustment for "increase in young" contradicts this, claiming no foxes were left untrapped in 1954. Clearly, one or the other or both of these views are wrong. In contrast, if the latter assumption is used, that the unmarked foxes were immigrants, then for a valid calculation of the populations the amount of adult, marked fox emigration must have been equal to this immigration. Probably both trap avoidance and movement were involved.

(5) There was no loss of marking on the foxes for the first year.

The ear tags used were designed for the purpose and were reasonably successful. If they failed most foxes retained some sort of scar on the foot, or in the ear where the tag pulled out, at least for the first year. After the tattoo kit was obtained all foxes were permanently marked.

(6) The relative trapability of the young and adults does not change during the time of the study.

In reference to the previously untrapped foxes this assumption is probably true. However, a fox that has once been caught will probably learn to some degree to avoid traps. Yet 28 foxes were recaptured within the first year of the study. Within 1954, 20 per cent of the foxes were recaptured. Within 1955, 13 per cent were recaptured. According to the average probability of survival (0.36) and expecting the 1954 recapture rate to occur again in 1955, the recapture rate of 1955 should have been only seven per cent. The difference between the expected (7%) and the actual (13%) proportion of recaptures for 1955 may be that some of the foxes forgot their former trap experience during the seven months interim between the 1954 and 1955 trapping periods. Still, some foxes avoided traps. Avoidance was readily apparent in the field where the tracks of foxes in the sandy soil showed that they were not caught even though being attracted by the scent. The figures comparing the proportion of the recaptures of the males and the intact females also indicated trap avoidance by the males.

(7) There is no marked change in the behavior of the sterilized females.

The scope of this study made it impossible to carry out a behavioral or physiological check on this assumption. The eight caged, sterilized females showed no obvious difference in behavior. On the Norias Plantation, a male and female remained paired although shifting their range after the female was hysterectomized. On the basis of what is known of the physiology of the canine uterus (Reynolds, 1949) it is possible to surmise that there were no physio-

logical changes in the sterilized foxes due to the hysterectomy.

(8) That no other factor such as climate, changes enough during the study to affect the age ratio.

Actually, although the weather data showed no marked changes during the time of the study, so little is known of the effect of climate on fox populations that some unsuspected, apparently minor change, might seriously affect the population.

(9) The observed reduction in the ratio of juveniles to adults from the first year to the second year was due to the sterilization of the female foxes.

This assumption is basic to the method and no other cause for a reduction of this ratio other than chance appears plausible.

CONFIDENCE LIMITS

Professor W. G. Cochran, Bio-statistics Department, Johns Hopkins University, provided the following description for determining the confidence limits for the age-ratio-reduction method for estimating populations.

"The error in the estimated total population arose from several sources: (1) any incorrectness in the biological assumptions on which the method is based, (2) sampling errors in the estimated ratio of juveniles to adults in the two years, (3) errors in the adjustments made to the number of adults in the second year on account of decreased trapability. Quantitative assessment of the degree of error from source (1) is difficult and requires special studies, this being true also of the marking and recapture methods. It is possible to give an approximate formula for the error due to source (2), as follows.

The unadjusted estimate of total population is

$$\hat{N} = \frac{2f_s \dfrac{p_1}{q_1}}{\dfrac{p_1}{q_1} - \dfrac{p_2}{q_2}}$$

where

f_s = number of sterilized females.
p_1 = proportion of juveniles in the 1st year. $q = 1 - p$
p_2 = proportion of juveniles in the 2nd year. $q = 1 - p$

The approximate coefficient of variation of N (i.e., ratio of the standard error to the mean) is

$$\frac{(\hat{F} - f_s)}{f_s}\sqrt{\frac{(1 - r_1)}{n_1\ p_1\ q_1} + \frac{(1 - r_2)}{n_2\ p_2\ q_2}}$$

where

$\hat{F} = \frac{\hat{N}}{2}$ = estimated female population.

n_1 = size of sample in first year.

r_1 = trapping success (proportion of total foxes captured) in the first year.

n_2, r_2 have the same meanings for the second year.

The standard error becomes low when the samples are large (n_1, n_2 large) or when the trapping success is high (r_1, r_2 near 1).

Sampling errors in the adjustments mentioned in (3) above will increase the standard error to some extent, so that this formula can be regarded only as indicating the *maximum* precision which the method can achieve. For computation purposes the formula can be rewritten

$$\frac{SE\ (\hat{N})}{\hat{N}} = \frac{(\hat{F} - f_s)}{f_s} \sqrt{\frac{n_1\ (1 - r_1)}{a_1\ j_1} + \frac{N_2\ (1 - r_2)}{a_2\ j_2}}$$

where a, j are the numbers of adults and juveniles.

Applying this formula to the adjusted Panacea data,

$$\frac{SE\ (\hat{N})}{\hat{N}} = \frac{(33 - 18)}{18} \sqrt{\frac{(60)}{(38)(22)}(.09) + \frac{(32)}{(18)(14)}(.32)}$$

The minimum standard error is about 18%.

The approximation formula becomes suspect when the standard error becomes high, say over 30%.

Applying the formula to the adjusted Norias data;

$$\frac{SE\ (\hat{N})}{\hat{N}} = \frac{(31 - 18)}{18} \sqrt{\frac{(63)}{(39)(23)}(.00) + \frac{(40)}{(21)(19)}(.22)}$$

The minimum standard error is about 22 per cent.

REPRODUCTION AND MORTALITY

In northern Florida the birth of the majority of young gray foxes is in March (Wood, 1958), about a month ahead of northern United States. Gray foxes are suspected of being monogamous at least for the year (Seton, 1909). In support of the monogamy statement, a pair of probably sibling foxes changed their range from one year to the next. The female fox had been sterilized. This means that in all probability these two foxes remained paired through a mating season

and denning season, at least until the advent of a new mating season, and in spite of a change in home range and an unsuccessful mating insofar as producing a litter was concerned. Incidentally, this case supports the assumption that there was no change in the behavior of sterilized females, for she apparently remained sexually attractive to her mate after the operation.

An average placental scar and embryo count compiled by Wood (1958), gave 4.56 as the average number of embryos per female in southern Georgia and northern Florida. The mean number of placental scars of foxes from the Norias and Sunnyhill plantations was 4.71. The mean number of placental scars in six females from the Panacea area, however, was only 3.33.

If it is assumed that the fox populations investigated in this study were stationary, that is, for each year the number born were equal to the number that died, and immigration was negligible or balanced by emigration, then we may determine the annual probability of dying for these populations.

On the Panacea area the ratio of juveniles to adults was 64 per cent. The average age of these juveniles was 7 months. Assuming a stationary population, the annual probability of dying of adult foxes was 0.64. Using the figure of 4.56 as the average number of young per female (Wood, 1958), the young then make up 69 per cent of the fox population. Again assuming a stationary population, and a constant adult mortality throughout the year, the probability of dying for juvenile foxes from uterus to trapability (average of 7 months) was 0.43. This probability of dying is low compared to other species and indicates that the care of the young by the adults is successful. By assuming a stationary population it is possible to calculate that the average longevity or life expectancy of a fox that reaches 7 months of age was about 18.5 months in this natural fox population.

The tooth wear system developed by Wood (1958) was applicable to the foxes of the Panacea area. The number of foxes in each age class, assuming a constant birth rate over the past years, and a constant death rate for each age group, is a result of the death rate for its age group. Table III shows the number of foxes in each age category for both years of the study, and their annual probability of dying.

The annual probability of dying was calculated for the Norias Plantation to be 0.63 for adult foxes and 0.43 for juveniles. The number of foxes in each age class and their annual probability of dying is listed in Table III. The average longevity of adult foxes on the Norias Plantation was 1.59 years or 19 months.

On the Sunnyhill Plantation the annual probability of dying of the foxes was similar to that of the Norias Plantation, being 0.61 for adult foxes and 0.47 for juveniles. Table III lists the numbers of foxes in each age class and their annual probability of dying for this plantation. The average longevity for adult foxes on the Sunnyhill Plantation was about 19.7 months.

HOME RANGE AND FAMILY AGGREGATIONS

The home range is that area occupied continuously by the fox for most of the year. Somewhat more extensive traveling occurs when the mating urge stirs them (Sheldon, 1950; Layne, 1956), but from the time they pair off until the next mating season approaches, the foxes confine themselves to their home range. The family aggregation is self explanatory and is distinguishable on an area because of its isolation from other families and foxes.

Probably the distance between captures and recaptures of the foxes and the diameters of the family aggregations gives a clue to the approximate size of the home range of the gray fox. Of the 141 foxes trapped and released on the three study areas, 28 were recaptured and released during the first year, and 18 were recaptured during the second year. It is apparent that the chance of getting recapture distances extending across the complete diameter of the home range of an individual fox is small. Conversely, the number of recaptures around the center of the home range should be most numerous. Table IV illustrates that the field data agree with this concept. The reason that no recaptures were made at the point of the first capture was due to the trapping procedure (seldom was a trap placed in the same place twice). The data indicate that the probable maximum diameter for the home range of the gray fox in this region was about two and one-half miles and the average was about two miles. The two foxes recaptured in 1955, three and three-quarters miles

TABLE IV.—Recapture distance and family aggregation diameters

Distances in miles	Number of recaptures within 1954	Number of recaptures from 1954 to 1955	Number of family aggregations 1954 & 1955
.00- .25	6	2	1
.26- .50	4	4	8
.51- .75	5	1	6
.76-1.00	4	0	4
1.01-1.25	5	1	1
1.26-1.50	0	3	1
1.51-1.75	2	4	0
1.76-2.00	1	0	0
2.01-2.25	0	0	0
2.26-2.50	1	0	0
2.51-2.75	0	0	0
2.76-3.00	0	0	0
3.01-3.25	0	0	0
3.26-3.50	0	0	0
3.51-3.75	0	2	0
3.76-4.00	0	0	0
11 miles	0	1	0
Total	28	18	21

from their 1954 point of capture possibly represents a shift in home range. In fact the 1955 data also probably show a slight shift in home range of about one half of the foxes. It is possible that a winter shuffle, as described by many writers, (e.g., Layne and McKean, 1956), resulted in a rematching of many pairs with their close neighbors and the dominant individual of the new pair pulled its new mate into its home range.

The family aggregation as used within this paper is a cluster of individuals within a small area as plotted on the map and probably represents members of a family unit. It was noticed during the trapping, that in some areas a number of foxes would be caught close to one another, and the group consisted of an adult male and female and a number of juvenile foxes. This group might be isolated from the nearest captured fox by as much as one mile. Consequently all the captures for both 1954 and 1955 were plotted on separate maps and designated as to age and sex of the fox. Twenty-one family aggregations could thus be reasonably well designated and several others might also have been added. The maximum diameters of these family aggregations are listed in Table IV. It can be seen that these data are also in support of the estimate arrived at for the home range of the gray fox based on recapture distances. Family aggregations caught in the summer were tighter in their grouping than those caught in the fall. Many of the scattered juveniles were caught late

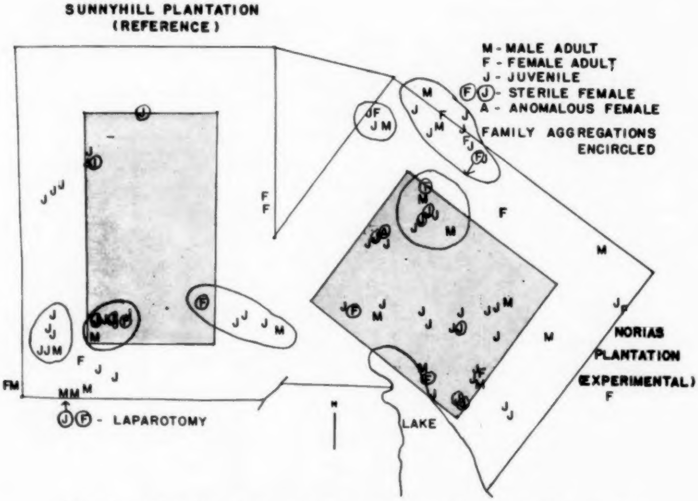

Fig. 3.—The distribution of the capture of foxes in 1954 on the Norias and Sunnyhill Plantations.

in the trapping period, and possibly represent the beginning of dispersal from the family unit. The average maximum diameter of the family aggregations was 0.74 miles. The relatively long duration of the maintenance of the family aggregation as a unit probably accounts for the low mortality of the juvenile foxes.

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The Diel Cycle of Stratification and Productivity in Two Lakes of the Chuska Mountains, New Mexico[1]

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ABSTRACT: Deadman and Whiskey lakes are shallow lakes having abundant rooted vegetation. They are located on the flat, rolling crest of the Chuska Mountains. The vertical plant stems and thermal density strata inhibited turbulence in the water columns of these lakes so that a discrete trophogenic zone developed each day during photosynthesis. This stratification was disrupted by descending density currents when the surface water was cooled each evening.

Because the daily stratification inhibits chemical interchange between the trophogenic zone and the tropholytic zone adjacent to the sediments, the rate of net productivity can be estimated from measurements of the diurnal accumulation of oxygen in the trophogenic zone. The mean rate of net oxygen production derived from three 20-hour studies of the cycle of stratification was 364 mg/m^2/hr, indicating that the net productivity among the rooted plants in these lakes is on the order of 1 g carbon/-m^2/day.

INTRODUCTION

The lakes scattered along the flat top of the Chuska Mountains are characteristically shallow and have an abundance of rooted aquatic vegetation. Three 20-hour series of observations were completed on Deadman Lake and Whiskey Lake, two of the largest of these lakes, during July and August, 1959. The studies revealed that very large thermal and chemical changes occurred regularly each day among the plants. Furthermore, these changes were associated with a diel cycle of thermal stratification.

Diel chemical changes are not only ecologically significant; they are also valuable indexes of productivity. Several papers have appeared recently (Jackson and McFadden, 1954; Odum, 1956; Verduin, 1956; Talling, 1957) in which daily fluctuations of oxygen and carbon dioxide have been utilized to evaluate the productivity *in situ* of natural waters. This approach to the study of productivity usually has been applied to phytoplankton communities, because the lower limit of the trophogenic zone among rooted aquatic plants often is difficult to identify. In Deadman and Whiskey lakes, however, the chemical changes associated with photosynthesis were observed to be

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confined within a surficial zone by the daily development of thermal stratification. Hence, oxygen fluctuations, although perhaps not carbon dioxide fluctuations, can also be used to estimate the productivity of these communities.

The Chuska Mountains, extending NNW for 95 km across the northern part of the Arizona-New Mexico border, are the major upland (elevation 2,700 to 3,000 m) on the Navajo Indian Reservation. The top of the range forms a relatively flat, rolling crest which in places is 2 to 5 km wide. The eastern edge of the crest is an abrupt escarpment from which the relatively undissected mountain-side slopes down to the Chaco Valley, more than 1,000 m below. On the west, the crest gives way to numerous canyons that lead down to the Defiance Plateau. Vegetational cover on most of the summit consists of an open ponderosa pine (*Pinus ponderosa*) forest that grades into stands of Douglas fir (*Pseudotsuga taxifolia*), blue spruce (*Picea pungens*), and subalpine fir (*Abies lasiocarpa*) along the north-facing slopes of the canyons. Below 2,400 m the ponderosa pine is replaced by the pinyon-juniper association. The range is capped by Chuska sandstone (Wright, 1956) which is pitted with hundreds of small basins, many of which contain water permanently, others only tem-

TABLE I.—Chemical analyses of waters from the Chuska Mountains (these analyses were performed by the U. S. Geological Survey Laboratory in Denver, Colorado, on water samples submitted by Dr. H. E. Wright; all values are in ppm unless otherwise indicated)

	Long Lake	Wide Lake	Basalt Lake	Boot Lake	Deadman Lake	Landslide Lake	Owl Spring
SiO_2	4.2	4.2	2.4	1.8	7.6	0.6	35.0
Al	0.1	0.2	0.5	0.6	0.3	0.3	......
Fe	0.1	0.2	0.3	1.5	0.1	0.3	......
Mn	0.0	0.0	0.0	0.0	0.0	0.2	......
Ca	19.0	9.6	24.0	29.0	17.0	11.0	60.0
Mg	4.4	2.9	9.7	6.8	3.9	1.9	11.0
Na	7.4	3.8	2.8	5.5	3.5	2.2	4.8
K	1.4	3.2	3.0	2.2	2.6	3.2	......
HCO_3	54.0	42.2	127.0	119.0	22.0	42.0	226.0
CO_3	10.0	0.0	0.0	0.0	26.0	0.0	0.0
SO_4	21.0	2.6	0.9	0.4	4.4	0.9	5.4
Cl	1.0	7.0	2.0	5.0	2.0	6.0	8.0
F	0.0	0.3	0.2	0.0	0.3	0.0	0.0
NO_3	0.0	0.0	0.0	0.0	0.0	0.0	0.5
PO_4	0.0	0.1	0.6	0.2	0.0	0.5	......
TDS 180°	91.0	77.0	108.0	......	104.0	74.0	......
TDS Sum	94.0	55.0	107.0	110.0	77.0	47.0	231.0
Hardness as $CaCO_3$	66.0	36.0	100.0	100.0	58.0	35.0	194.0
pH	9.0	6.8	7.0	6.9	9.9	6.5	......

porarily after periods of high precipitation. Chemical analyses from a number of lakes and springs in the region (Table I) show that these are carbonate-bicarbonate waters rather than saline, even though the lakes occupy closed basins and are rarely drained.

DEADMAN AND WHISKEY LAKES

Deadman and Whiskey lakes are two of the largest and most nearly permanent lakes in the Chuska Mountains. Deadman Lake (elevation 2,780 m) is located about 5 km west of Toadlena, New Mexico, equidistant from either end of the range and about 0.5 km from the eastern escarpment. The lake is roughly rectangular, about 380 m long and 300 m wide, with an area of 11 ha and an average depth of 0.6 m during the summer of 1959. The maximum depth recorded in 1958 was 1.25 m, but in July, 1959, the maximum depth was 0.8 m. There is no record that Deadman Lake has been recently dry. A mat of *Chara* 15 to 30 cm thick covered the bottom of the southern half of the lake, but the vegetation in the northern half comprised floating and emergent stands of *Eleocharis macrostachya, Myriophillum exalbescens,* and *Polygonum amphibium* with a *Chara* understory.

Whiskey Lake (elevation 2,700 m) is located near the southern end of the Chuska Mountains, south of Washington Pass.[2] It is 850 m long, 250 m wide, with an area of 21 ha. The depth was 1.2 m during July and early August, 1959, but a maximum of 1.7 m was recorded in 1958. Although Whiskey Lake was dry in 1956, it filled to the level of its outlet in 1957. Bunches and beds of bullrush (*Scirpus acutus*) were scattered all over the lake except in a zone 8 to 10 m wide along its circumference. In this peripheral zone and in almost all of the rest of the lake there was a dense growth of *Polygonum amphibium* and *Myriophyllum exalbescens.* Emergent or floating vegetation was absent in a few areas, but even these had a bottom mat of *Chara.*

Although horses and cattle were seen browsing in the lakes occasionally, and the Navajo allow their herds of sheep and goats to graze in the meadows around the lakes, the aquatic vegetation does not seem to have been damaged excessively. Larval and adult salamanders (*Ambystoma tigrinum*) were abundant in both lakes. Whiskey Lake was stocked with 16,000 rainbow trout fingerlings in May, 1958, and by August, 1959, many of these had grown to the rather extraordinary length of 30 cm.

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[2] The lake discussed here is located on the Tohatchi quadrangle (1:62,500) published by the United States Geological Survey. An artificial lake located 10 km NW of Crystal, New Mexico, at the western base of the Chuska Mountains, is also called Whiskey Lake, according to the Shiprock, New Mexico-Arizona topographic sheet (1:250,000), but it is called Little White Cone Lake on the Sonsuela Buttes, Arizona-New Mexico quadrangle (1:62,500).

MATERIALS AND METHODS

A raft composed of two sheets of plywood lashed to four truck tire inner tubes served as a sampling platform. While collections were being made the fore and aft ends of the raft were firmly lashed to poles driven into the bottom. Since one of the poles extended about 1 m above the water surface, the collecting station could be located precisely and easily, even at night.

Water samples for the determination of oxygen, temperature, pH, and carbon dioxide were obtained with a modified Irwin Sampler (Welch, p. 204-206). This consisted of a one-liter reservoir bottle connected by rubber tubing to a series of two 250-ml sample bottles. Water was raised from the lake through an intake tube into the series of bottles by withdrawing air from the reservoir bottle with a small plunger-type bilge pump. In order to obtain water from specific depths, the free end of the intake tube was positioned at a point on a graduated iron rod, one end of the rod and the attached tubing were lowered through a slot in the center of the raft, and the end of the rod was pressed against the bottom while water was entering the intake tube. This collection technique permitted sampling the water column at any depth with minimal disturbance. The oxygen content of a stratum of water was determined from the water in the first sample bottle of the series, pH from the second, and temperature from the reservoir bottle.

The oxygen concentration was determined using the unmodified Winkler method. A Beckman model N pH meter was used to meas-

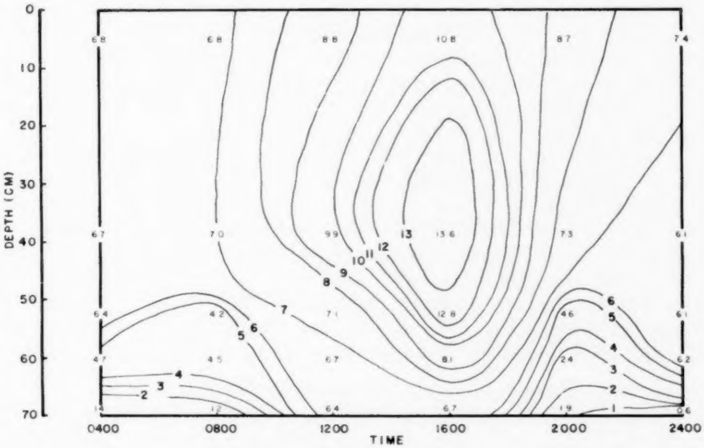

Fig. 1.—Time-depth diagram of oxygen distribution in Deadman Lake beginning at 0400 hours, July 13. The numbers in small type on the diagram represent the measured concentrations in ppm.

ure hydrogen ion concentration. Temperatures were measured with a simple mercury-bulb thermometer calibrated in degrees. A more precise means of determining temperatures would have been desirable, but fortunately thermal changes were so large that this thermometer was adequate to determine the course of thermal variations. Changes in carbon dioxide concentrations were determined from pH titration curves according to the method proposed by Verduin (1956), using N/44 H_2SO_4 as the titrating agent. The carbon dioxide concentration was assumed to be equivalent to the volume of standard acid necessary to establish the pH in the water samples. The shortcomings of this technique of determining carbon dioxide among rooted aquatic plants will be discussed below.

RESULTS

The diel cycle of stratification among the plants of these lakes was first observed during 20-hour studies of oxygen fluctuations. The results of a study on Deadman Lake between 0400 hours and midnight, July 13, are shown in a time-depth diagram, Figure 1. The depth of the water was 68 cm. A vigorous growth of *Chara* occurred below 30 cm, and the stems of a few *Myriophyllum* plants extended up to the 20 cm depth.

In the morning, before 0800 hours, there was little stratification in the water above 50 cm. Oxygen was rather uniformly distributed, ranging from 6.4 to 6.8 ppm. At greater depths, between 50 and 68 cm, the oxygen concentration decreased rapidly to less than 1.4 ppm near the sediments, and the trend was toward oxygen depletion until 0800 hours.

Oxygen concentration increased at all depths after 0800 hours, and a distinct oxygen stratification developed by 1600 hours. Maximum oxygen content among the *Chara* was 13.6 ppm during stratification, and oxygen increased to 6.7 ppm even next to the bottom. The average oxygen increase between 0800 and 1600 hours was 6.0 ppm in the upper 60 cm of the water column.

A severe thunderstorm with strong gusts of wind occurred between 1600 and 2000 hours. By 2000 hours the stratification was deteriorating in the upper 50 cm, and the uniform oxygen distribution that occurred early the previous morning again prevailed by midnight. In the early evening the oxygen began to decrease at 50 and 60 cm, but before midnight there was a surprising oxygen increase in this stratum. It was largely this anomalous oxygen increase during the hours of darkness that indicated the desirability of more complete investigations including data on temperature, pH, and carbon dioxide.

THE RELATIONSHIP BETWEEN VEGETATION AND THE STRATIFICATION

A diel oxygen stratification of the type occurring in Deadman Lake might be expected in any stable body of shallow water where there is abundant photosynthesis each day. In order to determine if the stability and stratification in the water column could be attributed

to the rooted vegetation, vertical series of temperature, pH, and oxygen determinations were made in two areas of Whiskey Lake. One station, with an area of about 10 m^2, was free of rooted vegetation except for a bottom mat of *Chara* 10 to 15 cm thick; at the other area, a dense growth of *Myriophyllum* and *Polygonum* reached the surface. The depth was similar in both areas, 114 and 122 cm, respectively. The data were gathered between 1400 and 1600 hours, July 30, when the weather was clear and sunny, and the air temperature was 23° C.

The different conditions in the two areas are shown in Figure 2. Temperatures in the open water decreased from 23° at the surface to 22° at the bottom, and oxygen decreased gradually from 9.35 ppm at the surface to 6.58 ppm at the bottom. The pH of the water

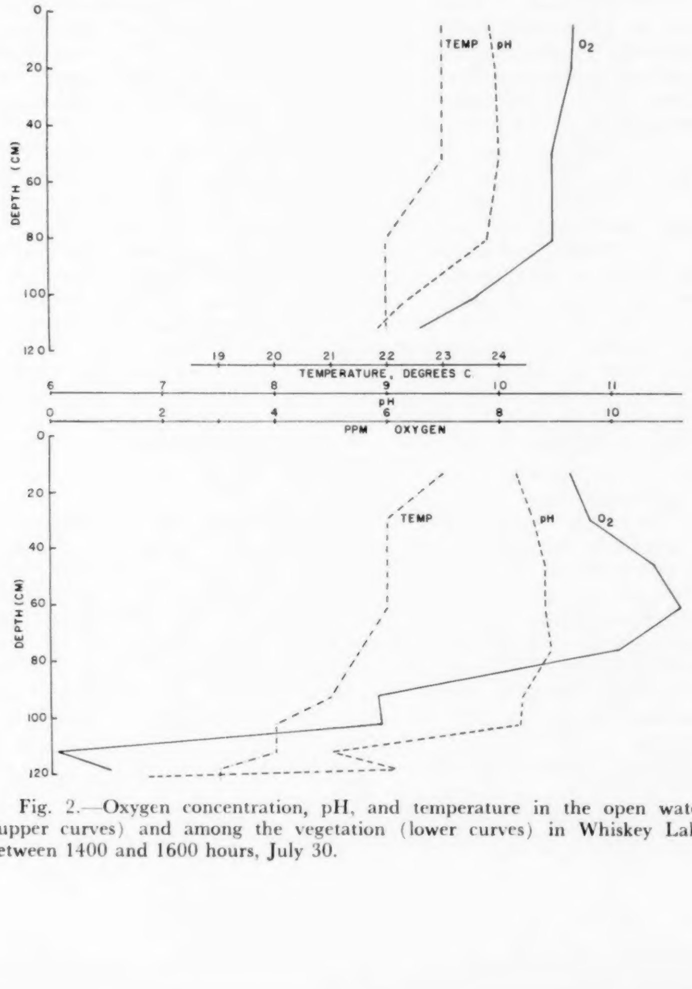

Fig. 2.—Oxygen concentration, pH, and temperature in the open water (upper curves) and among the vegetation (lower curves) in Whiskey Lake between 1400 and 1600 hours, July 30.

column, however, was somewhat less regular. The pH was 9.92 at the surface, 10.01 at 51 cm, and 8.93 at the bottom.

The conditions among the plants were considerably different from conditions in the open water. The temperature data indicate a distinct thermal stratification. The surface water temperature was the same as the air temperature, 23° C, but the bottom water temperature was only 19°, 3° colder than the bottom temperature in the open water. There was also a definite oxygen stratification among the plants in which oxygen concentration varied between 8.81 ppm at the surface, 11.21 ppm at 60 cm, and 0.96 ppm at the bottom. All pH values in the upper 100 cm were greater than 10, with a maximum of 10.45 at 76 cm. The water became less alkaline at depths below 100 cm, with pH decreasing to 6.88 at the bottom.

These data from two areas in Whiskey Lake compare favorably with the results obtained by Buscemi (1958, Fig. 3) in Parvin Lake, Colorado. He found uniform oxygen distribution in the surficial meter of water, above a mat of *Elodea*. In the deeper water among the plants, between 1.2 and 2.2 m, oxygen was stratified as among the *Myriophyllum* and *Polygonum* in Whiskey Lake.

It is evident from the comparison of these two areas in Whiskey Lake that the stratification was a phenomenon associated with the rooted plants. Apparently the vegetation reduced the effects of the wind, inhibiting the lateral water movement and turbulence that would normally result from wind action. Consequently the limited circulation enabled thermal density strata to develop as the water absorbed solar radiation. These density strata, in turn, restricted vertical water movements. The inhibitors of turbulence — the vertical plant stems and horizontal density strata — enabled a thermal gradient of 4° to develop in the water column in mid-afternoon. Moreover, oxygen accumulated and pH became very alkaline in the strata where there was sufficient light for photosynthesis. Evidently the plants obtained carbon dioxide from bicarbonates, because free carbon dioxide could hardly exist at the alkaline pH observed in the region of photosynthesis.

Vaas and Sachlan (1955), who studied diurnal fluctuations in shallow fish ponds in Indonesia, measured daily temperature changes in a water-filled pit near their laboratory. The diameter of the pit was 2 m, and the depth was 2 m. The average of 30 series of temperature readings (their Table 1) showed that the water in the pit was homothermal at 0730 hours, but that there was a distinct thermal stratification by 1530 hours involving a thermal gradient of 4.9° in the surficial meter of water. The temperature at the bottom did not increase during this time period because of turbidity (Secchi disc reading = 80 cm). The authors concluded that "wind action is practically nil and absorption of sunlight is the principal source of heat."

The similarity between the thermal gradient among the water plants of Whiskey Lake and the gradient in the pit indicates that

turbulent heat transfer is inhibited as effectively by the vegetation as if the water column were bounded by walls like those of the pit.

DIEL CYCLE OF STRATIFICATION IN WHISKEY LAKE

A detailed 20-hour study of temperature, pH, dissolved oxygen, and carbon dioxide among the rooted plants in Whiskey Lake was made on August 2, 1959, to obtain more information about the diel cycle of stratification. Collections were made at 4-hour intervals between 0400 and 2400 hours at depths of 5, 30, 60, 90, 110, and 120 cm.

The temperature trends at 5, 60, and 120 cm are shown in Figure 3. At 0400 hours the lake was virtually homothermal with temperatures between 16.5° and 17.0° C at all depths. Subsequently, between sunrise (0537 hours) and 0800 hours, the entire water column warmed an average of 1.8°. Between 0800 and 1200 hours, however, the surface water was heated more rapidly than the lower depths, and thermal stratification developed. Since most of the temperature increase was in the upper 60 cm, and since air temperatures were lower than water temperatures during the warming phase, the temperature increase must have been caused by direct absorption of solar radiation rather than by contact with the atmosphere. After 1200 hours the surface water began to cool. This was undoubtedly the result of a cloud cover that developed late in the morning and prevailed throughout the rest of the day. By 2000 hours, one-half hour after sunset, the lake was again homothermal.

The temperature trends at 120 cm perhaps indicate that there was a net loss of heat from the bottom water to the sediments except when the entire water column was warming in the morning and again when there was circulation as the lake became homothermal in the evening.

The changing chemical conditions during the study period are shown in Figures 4 and 5. Throughout the day, conditions in a zone

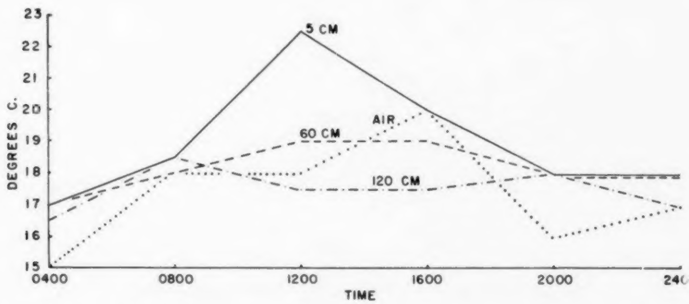

Fig. 3.—Air temperatures and water temperatures at 5 cm, 60 cm, and 120 cm in Whiskey Lake between 0400 and 2400 hours, August 2.

above 90 cm were markedly different from the conditions between 90 and 120 cm. In the surficial zone (0 to 90 cm) oxygen content varied from 5.2 to 10.2 ppm, pH varied from 9.60 to 10.40, and free carbon dioxide was as low as −37.1 ppm. Below 90 cm the oxygen content was always less than 5.2 ppm, becoming even less abundant or absent near the sediments. Also, pH was neutral or slightly acid in the bottom zone, varying between 7.91 and 6.18, and free carbon dioxide concentrations were as high as + 11.5 ppm.

Another difference between the two zones is evident in the time-depth diagram of oxygen distribution (Fig. 5). A stable microstratification with a steep oxygen gradient persisted in the bottom zone during the entire study period, but oxygen stratification developed in

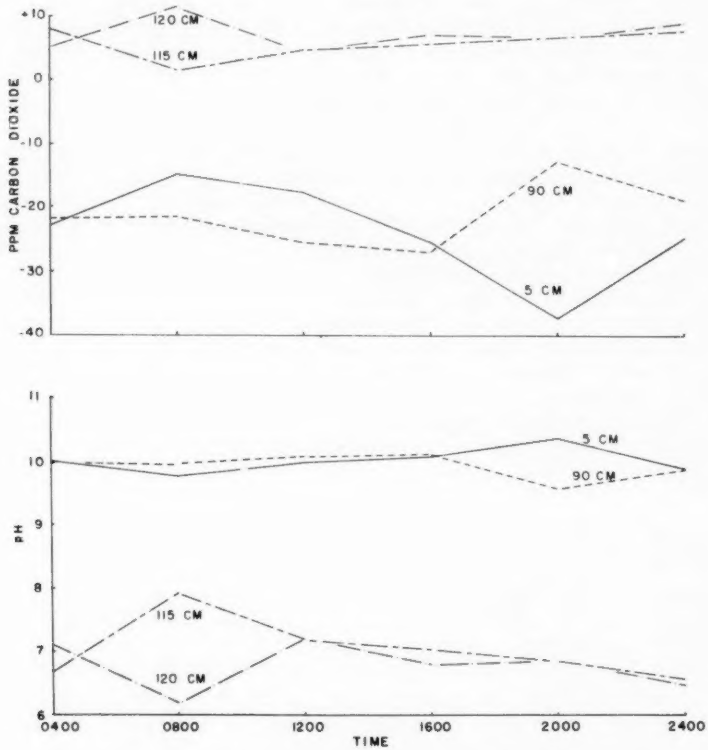

Fig. 4.—The pH and apparent free carbon dioxide concentration in Whiskey Lake beginning at 0400 hours, August 2. The values at 30 and 60 cm, which virtually coincide with the values at 5 cm, have been omitted for clarity of presentation.

the surficial zone only in conjunction with thermal stratification. At 0800, when the water column was homothermal, oxygen was uniformly distributed in the surficial 90 cm, ranging between 6.16 and 6.40 ppm. The pH was also rather uniform, varying from 9.56 to 9.97. Between 0800 and 1600 hours, with the onset of thermal stratification and with increasing photosynthesis, the oxygen concentration increased to 9.13 ppm at 5 cm, to 9.83 ppm at 30 cm, but to only 6.34 ppm at 90 cm. The average oxygen increase in the surficial 90 cm was 2.10 ppm by 1600 hours. During these 8 hours the average pH increased from 9.76 to 10.02, corresponding to the removal of 12.8 ppm carbon dioxide. It should be noted that the oxygen content at 90 cm did not continue to increase after noon; it is probable that there was insufficient light for continued photosynthesis at that depth, apparently because of the overcast sky.

By 2000 hours the water column was again homothermal, and although the chemical stratification was observed to be best developed at this time, it was presumably even more distinct sometime during the previous four hours.

A study of the changes below 90 cm indicates the mechanisms of the destruction of chemical stratification in the surficial zone. Although there were large increases of pH and oxygen content during daylight in the surficial zone, the pH and oxygen concentration decreased between 90 cm and the bottom, indicating the stability of the microstratification adjacent to the sediments. But after 2000 hours, when oxygen and pH began to decrease near the surface, oxygen concentration at 90 cm increased from 5.20 to 8.81 ppm, and pH increased from 9.60 to 9.90. Evidently this was the result of the descent of warm water, rich in oxygen and with high pH, because the bottom

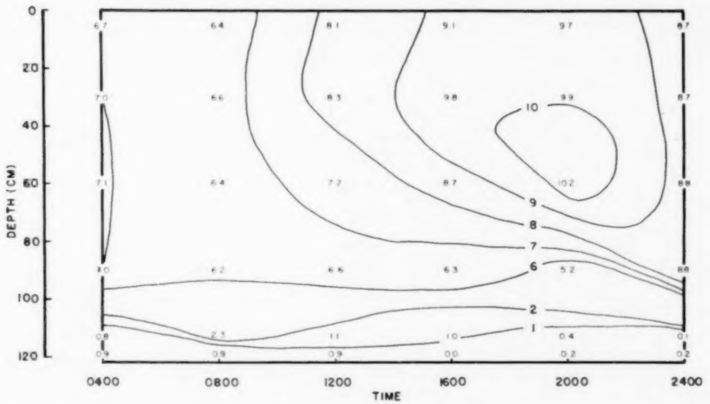

Fig. 5.—Time-depth diagram of oxygen distribution (ppm) in Whiskey Lake between 0400 and 2400 hours, August 2.

water temperature increased 0.5° between 1600 and 2000 hours. This phenomenon is reminiscent of the oxygen increase observed after dark near the bottom of Deadman Lake. The oxygen increase in both instances apparently was due to the previous cooling of the surficial water. Instability resulting from the surficial cooling enabled oxygen-rich density currents to descend, increasing the oxygen content near the bottom of the water column at the expense of the overlying water. It seems there was only a limited transport of oxygen to the bottom-most strata, because the bottom 15 cm contained at most 1 ppm oxygen at night, whereas the rest of the water column contained about 7 ppm. Evidently a persistent, complete circulation was prevented by the re-establishment of density barriers after 2000 hours when bottom temperatures decreased. Thus, oxygen transport to the bottom was not extensive most of the night; there was circulation, but only in the surficial zone of the water column, and the environmental differences between the upper and lower zones persisted during the entire diel cycle of stratification.

FURTHER STUDIES ON DEADMAN LAKE

Deadman Lake was studied again on August 12 and 13, and temperature, pH, and carbon dioxide data were gathered in addition to oxygen data. During the month since the previous visit, the depth of Deadman Lake had decreased from 70 cm to 60 cm. As a result, the stem tips of the *Myriophyllum* and *Chara* mat floated limply on the surface.

The temperature data (Fig. 6) revealed a thermal regimen similar to that of Whiskey Lake: the water column was homothermal in the morning, and stratification developed later in the day only to be disrupted in the evening. At 0800 the temperature at all depths was between 15° and 16°. After differential warming of the water column between 0800 and 1600 hours, the surface temperature was 21°, and the bottom temperature was 17.5°. This stratification was not dissi-

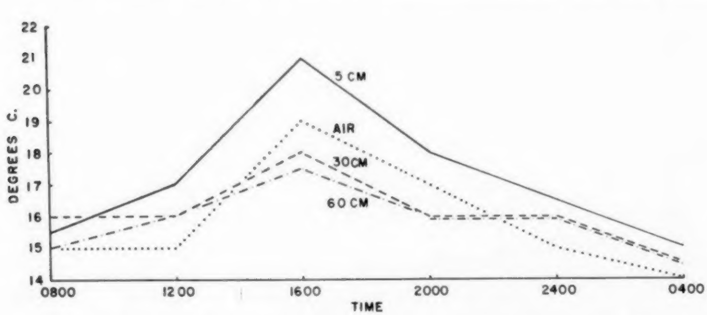

Fig. 6.—Air temperatures and water temperatures at 5, 30, and 60 cm in Deadman Lake, August 12.

pated until midnight. Even then the surface temperature was 16° and the remainder of the water column was 15.5°. After midnight the temperature of the water column continued to decrease, falling to 15° at 0400.

The oxygen, pH, and carbon dioxide data (Figs. 7 and 8) indicate a rather continuous gradient of decreasing oxygen and pH, and increasing carbon dioxide between the surface and the bottom. Although the chemical gradient was very steep between 40 and 50 cm, the upper and lower zones were less distinct than in Whiskey Lake, chiefly because there was some photosynthesis relatively close to the bottom. The gradient involved oxygen concentrations as high as 11.76 ppm at the surface to 0.0 ppm at the bottom. The pH varied between 9.61 and 10.35 at the surface and between 6.98 and 7.95 at the bottom. There was appreciable free carbon dioxide only between 50 cm and 60 cm.

As in previous studies of Deadman and Whiskey lakes there was a diel cycle of oxygen stratification associated with the development

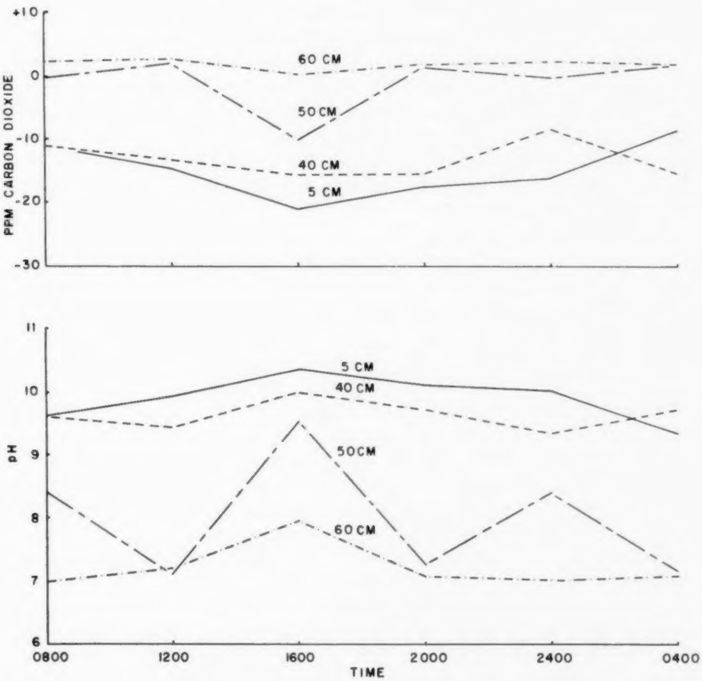

Fig. 7.—The pH and apparent free carbon dioxide concentrations in Deadman Lake between 0800 hours, August 12, and 0400 hours, August 13.

and disruption of thermal stratification. In the morning (0800 August 12, and 0400 August 13), oxygen distribution in the surficial 40 cm was uniform, averaging 5.0 ppm. But surface oxygen increased to 11.76 ppm by 1600, and the oxygen content at 40 cm increased to 7.75 ppm. This involved an average oxygen increase in the surficial 40 cm of 4.5 ppm.

The oxygen stratification deteriorated much more slowly than when it was previously observed, persisting until after midnight when the water column again became homothermal. This is not particularly surprising in view of the extraordinary denseness of the vegetation. Also, the thunderstorm on July 13 no doubt contributed to the premature disruption of the stratification that had been previously observed. Once again the disruption of stratification was associated with the peculiar nocturnal oxygen increase near the bottom of the water column, evidently another indication of the descending density currents discussed in connection with the study of Whiskey Lake.

The most obvious difference between Whiskey Lake (Fig. 5) and Deadman Lake (Fig. 8) is the oxygen increase at the bottom of the water column in Deadman Lake at 1600 hours. The lesser depth of Deadman Lake is perhaps one reason for this, but the differences of vegetation are probably also involved. Most of the plants in Deadman Lake were *Chara* and *Myriophyllum* with abundant foliage down to the bottom of the water column. In Whiskey Lake, however, the vegetation was mostly *Polygonum* with floating leaves and *Myriophyllum* with few leaves below 80 to 100 cm. Therefore, even if sunlight penetrated to the bottom of Whiskey Lake, there was reduced photosynthetic tissue.

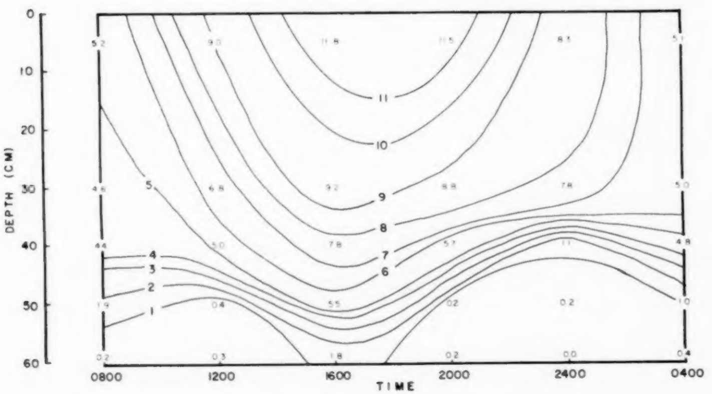

Fig. 8.—Time-depth diagram of oxygen distribution (ppm) in Deadman Lake between 0800 hours, August 12, and 0400 hours, August 13.

CALCULATIONS OF PRODUCTIVITY

All three of the studies discussed here encountered a gradient of decreasing oxygen, pH, and temperature and increasing free carbon dioxide with increasing depth among the plants. The gradient became particularly steep near the bottom of the water column so that two distinct zones were discernible. An upper trophogenic zone included in surficial 2/3 or 3/4 of the water column. Here there was as much as 10 to 13 ppm oxygen, and pH was very alkaline — as high as 10.4. Beneath the trophogenic zone there was a tropholytic zone in which oxygen concentration was typically less than 2.0 ppm. Respiration was the dominant process here, and pH was neutral or slightly acid as a consequence of carbon dioxide production. These zones preserved their identity throughout the sampling periods in the August 2 study of Whiskey Lake and the August 12 study of Deadman Lake. The zonation was also evident during the morning and evening when Deadman Lake was studied on July 13 (Fig. 1). But because vegetation was concentrated near the bottom of the water column, oxygen concentration increased considerably in the "tropholytic" zone during the afternoon. However, it is evident from the time-depth diagram that the tropholytic zone rapidly regained its identity by 2000 hours.

Buscemi (1958, Fig. 4), in his study of the environment among *Elodea,* also observed this zonation. He described an upper "photosynthetic zone" and a lower "respiratory zone."

Superimposed upon this zonation was a diel cycle of thermal and chemical stratification that involved primarily the trophogenic zone. The elements of the cycle — uniform temperature and distribution of oxygen in the morning, development of thermal and chemical stratification during daylight, and destruction of stratification in the evening — were clearly evident in both lakes.

If the daily development of thermal density strata and the accumulation of oxygen indicate the stability of the water column, then because density stratification inhibits chemical interchange between strata, the chemical changes in the trophogenic zone can be used to estimate the rate of primary production *in situ.* Talling (1957), who studied diurnal changes in African waters, pointed out that this method has advantages because of the short time intervals involved, provided that the waters are sufficiently productive to elicit measurable changes. He also stated that there are fewer errors of defining the depth of the productive water column where photosynthetic changes are confined within thermal density strata. Attempts to estimate productivity by measuring oxygen changes in light and dark bottles have been criticized (Pratt and Berkson, 1959) and are usually considered to give low estimates (Pomeroy, 1960) because of limited water circulation and excessive bacterial respiration in the bottles. The chief shortcoming of measuring productivity *in situ* from diurnal changes, however, is that it is difficult to determine the amount of gaseous exchange between the trophogenic and tropholytic strata and

between the trophogenic stratum and the atmosphere. The loss to the atmosphere decreases with decreasing turbulence in the water column. Because of the plants, the surface of the Chuska Mountain lakes usually remained unruffled, even during high winds, so the loss of oxygen to the atmosphere is probably a relatively minor source of error. Probably more oxygen was lost from the bottom of the trophogenic zone. This was undoubtedly the case during the first study of Deadman Lake when oxygen was produced throughout the length of the water column, with no tropholytic zone to insulate the trophogenic zone from the sediments. Although it is believed that the stability of these water columns inhibited the mechanisms of oxygen loss, the following calculations of productivity must be regarded as conservative estimates.

Because the oxygen increase in the water during daylight is the total oxygen produced less any oxygen utilized in respiration, the rate of oxygen accumulation is a measure of "net" productivity. It has been mentioned that considerable interchange between the trophogenic and tropholytic zones occurred during isothermal mixing after sunset. As a consequence the oxygen content near the bottom of the water column actually increased at night. This peculiarity makes it impossible to determine the respiration rate from the available data; consequently, gross production also cannot be determined.

One of the motives for obtaining data concerning pH and carbon dioxide fluctuations was to obtain an additional measurement of productivity in terms of carbon dioxide uptake. The very high pH values complicated this attempt, however. In the first place free carbon dioxide cannot be present in waters as alkaline as these. According to Hutchinson (1957, p. 657) the carbon dioxide at pH 10.0 is present as 76 per cent bicarbonate and 24 per cent carbonate. The disturbing factor is the relative insolubility of carbonates. On August 6, determinations of methyl orange alkalinity in Whiskey Lake showed the concentration of bound carbon dioxide (carbonate) to be 32.2 ppm at the surface, 31.6 ppm at 60 cm, and 39.0 ppm at the bottom. The high carbonate value at the bottom suggests that carbonates precipitated out of the trophogenic zone and dissolved again near the bottom. Thus, carbon dioxide was removed from the trophogenic zone not only by photosynthesis but also by chemical precipitation.

The estimation of carbon dioxide by means of pH and titration curves is a method usually employed in studies of phytoplankton in open water where the pH usually varies between 7 and 9. Recently a controversy has arisen (Beyers and Odum, 1959; Verduin, Beyers, and Odum, 1960) over the relative merits of using carbon dioxide water instead of strong acid or base to prepare the titration curves. The issue apparently is irrelevant here, since all the curves they discuss are identical when the pH exceeds 8.0, regardless of the titrating agent.

However, even if the titration curves represented the empirical

relationship between pH and alkaline substances in the water, there is little doubt that the pH increases during photosynthesis represented not only carbon dioxide removal but also hydroxide production. Arens (1936) demonstrated that when aquatic plants assimilate calcium bicarbonate they release an equivalent amount of calcium hydroxide to the water. The pH-titration curve method of estimating production presupposes that a pH increase represents carbon dioxide removed by photosynthesis; but the liberation of hydroxide would also increase the pH, and the resulting estimate of carbon dioxide uptake would be too large by an amount equivalent to the hydroxide.

The quantities of carbon dioxide removed and oxygen produced in the trophogenic zone of Whiskey Lake between 0800 and 1600 hours, August 2, are shown in Table II. It is clear that if the carbon dioxide changes are used to calculate productivity, the value is more than 5 times larger than an estimate based on the amount of oxygen produced. The oxygen data are considered more reliable because they are not subject to the uncertainties associated with the carbon dioxide data.

In view of these considerations, the following calculations of net productivity are based on the accumulation of oxygen in the water column between 0800 and 1600 hours. The oxygen increase in the entire water column is utilized for the July 13 study of Deadman Lake because there was considerable oxygen production even next to the bottom. But for Whiskey Lake and the second study of Deadman Lake, the calculations are based on the oxygen increase in the trophogenic zones. Oxygen produced has been converted to carbon fixed assuming a photosynthetic quotient (O_2/CO_2) of 1.25 as recommended by Ryther (1956). The results of the calculations are shown in Figure 9.

TABLE II.—A comparison of calculations of productivity based on oxygen production and apparent carbon dioxide uptake in various strata of the trophogenic zone of Whiskey Lake on August 2

	Chemical changes in trophogenic zone, 0800-1600 hours				Carbon fixation rate (mg $C/m^3/hr$)	
Depth	ppm O_2 increase	Apparent CO_2 decrease (ppm)	O_2 production rate (mg $O_2/m^3/hr$)	Apparent CO_2 uptake rate (mg $CO_2/m^3/hr$)	Calculated from O_2 data	Calculated from CO_2 data
Surface	2.78	10.65	347	1331	104	362
30 cm	3.23	22.08	404	2760	121	751
60 cm	2.22	13.24	280	1655	84	450
90 cm	0.18	5.60	22	700	6	191

In Deadman Lake 4.14 g $0_2/m^2$ were produced during the 8 hour period on July 13. The arithmetic mean rate of production was 517 mg $0_2/m^2/hr$. These values represent carbon fixation amounting to 155 mg $C/m^2/hr$. This production rate was accomplished by vigorous, growing vegetation during a very sunny day. By way of comparison, only 2.51 g oxygen were produced in 8 hours on August 12, a mean rate of 312 mg $0_2/m^2/hr$. or 94 mg $C/m^2/hr$. At the time of this study the *Myriophyllum* had set fruit, and the sky was often overcast. It is interesting that more oxygen was produced in the bottom 10 cm than immediately above. It is perhaps significant, then, that this was the only depth containing free carbon dioxide. Steemann Nielsen (1946) has shown that when free carbon dioxide is the carbon source, the photosynthetic rate of *Myriophyllum* is greater than when bicarbonate is the carbon source. Whiskey Lake produced 2.01 g $0_2/m^2$ between 0800 and 1600 hours, August 2. The mean rate was 261 mg/m^2 (78 mg C/m^2) per hour.

Although the rooted plants have been emphasized in this study, chiefly because of their role in the cycle of stratification, it is not to be inferred that they are considered to be the most important from the standpoint of production. In fact, Pomeroy (1960) has shown that the marine spermatophytes, *Thalassia* and *Syringodium*, in Boca Ciega Bay, Florida, are probably no more productive than either of the other autotrophic components of the community — the benthic microflora and the phytoplankton. Where the water was 2 m deep, total community gross production was about 500 mg $0_2/m^2/hr$. Pomeroy considers this a low value because he obtained his data by using bell jars and the light-dark bottle technique.

The average net productivity derived from the three studies in the Chuska Mountain lakes was 364 mg $O_2/m^2/hr$ (109 mg

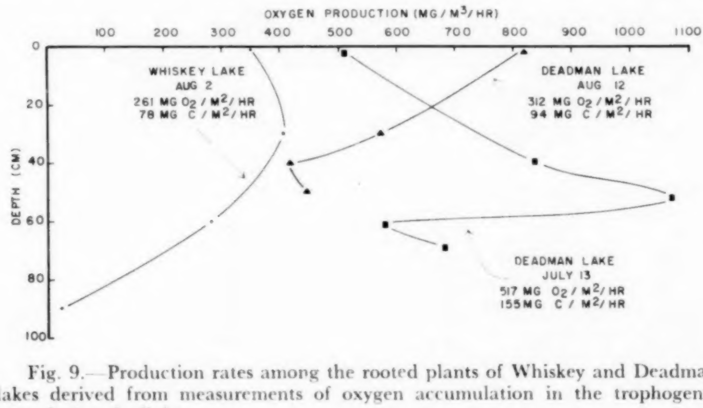

Fig. 9.—Production rates among the rooted plants of Whiskey and Deadman lakes derived from measurements of oxygen accumulation in the trophogenic zone during daylight.

$C/m^2/hr$), approximately 1 g $C/m^2/day$. The gross productivity would be higher than this value by an amount equivalent to the oxygen removed by the respiration of organisms in the water column and the oxygen lost to the atmosphere, the tropholytic zone, or the sediments.

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Dye Excretion as a Method for Determination of Small Mammal Home Ranges

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ABSTRACT: One hundred and twenty dyes and biological stains were tested in the laboratory for possible use in determining home ranges by excreted dyes. Dyes were mixed with beeswax, made into pellet form, and placed subcutaneously in *Mus musculus* and *Microtus ochrogaster*. Nine dyes colored the urine for four or more days (using 60-95 mg pellet) and did not depress activity as measured by activity wheels.

In field tests, dropping boards covered with filter paper were placed in a grid for recovery of colored urine from *M. ochrogaster* implanted with pellets. Home ranges calculated from the excreted dye spots corresponded closely to home ranges calculated from live trapping data for the same animals (using minimum area method).

Dyes in the same color range were found to be usable on different animals in the same area if one changed color when drops of weak acid or base solution were placed on the spots.

Most techniques designed to determine the home ranges of small mammals utilize some type of live trapping and recapture procedure. Many criticisms have been leveled against this method (Davis, 1953) but no clearly superior technique has replaced it.

The purpose of this study was first to develop a new method for determining home ranges which would eliminate some of the objectionable features of live trapping studies. The procedure developed was to implant pellets of dye into animals and determine movement by recording colored urine spots on dropping boards (Emlen *et al.*, 1957). Secondly the home ranges of some individuals were determined by conventional live trapping methods and then by the new technique to compare results obtained by these methods.

MATERIALS AND METHODS

LABORATORY

Initially 120 dyes were screened to determine their usefulness. Each dye was separately tested by preparing a pellet composed of a 1:1 ratio of dye to beeswax. Beeswax was used to form a matrix which prevented crumbling, and also slowed and prolonged absorption of dye from the pellet. Homogeneous mixing of dye and beeswax was accomplished by placing the weighed mixture of beeswax and dye granules in a paraffin oven at 56° C until the beeswax melted. This semi-liquid mixture was then removed from the oven and stirred with a glass rod until it hardened. The quantity of dye-beeswax preparation desired for a pellet was weighed in milligrams on a Roller-Smith torsion balance and then placed in a glaze-finished crucible for pulverization by a pestle.

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Preliminary experiments indicated that dye pellets placed under a rodent's skin were rapidly encapsulated by connective tissue, and within 2-4 days absorption and excretion of the dye largely ceased. It was found that when 8 mg of cortisone acetate powder were added to 50 mg of dye-wax preparation, encapsulation was retarded until about 14 days after pellet implantation. The thoroughly mixed dye-beeswax-cortisone preparation was made into a compact cylindrical pellet by tamping the mixture into a hole in a brass block. The diameter of the dye pellets thus formed was 2.38 mm (3/32 inch). Each pellet was brought to the desired weight or length by cutting portions off the end with a scalpel.

Laboratory white mice (*Mus musculus*) were used for the preliminary screening of the dyes. The pellets used in laboratory mice weighed from 35-40 mg. Each pellet was inserted subcutaneously into lightly anesthetized mice through a small incision in the dorsal skin about one inch anterior to the base of the tail. Then it was moved forward beneath the skin with a stroking action of the fingers to an infrascapular position. A single, small surgical clamp or a drop of celloidin was sufficient to close the incision.

Mice containing dye pellets were placed in wire-bottomed cages with food and water available at all times. A large piece of white filter paper was placed under each cage so that the urine could be checked for dye coloration. The criteria set for the screening tests were that the dye should color the animal's urine for several days (arbitrarily about seven), and that the dye should not produce any apparent adverse effect on the animal. If a dye did not meet these conditions it was discarded without further testing. Filter papers were changed at 24-hour intervals after pellet implantation until the urine spots no longer displayed any dye coloration.

Dyes that gave promising results were tested on specimens of *Microtus ochrogaster*. This second screening procedure was the same as that used in the laboratory mice. The pellet weights used in adult *Microtus* were from 65-90 mg.

Tests in activity wheels were conducted to determine the effect of dye pellets on a vole's activity. The number of revolutions for each 24-hour period was recorded throughout the activity experiments. After the normal activity of each specimen was obtained for a period of seven days, a pellet was implanted, and the individual's activity observed for another seven day period. Animals were weighed before being placed in the activity wheels, at the time of pellet implantation, and after the experiment was concluded, to give another index of the animal's health. Only male *Microtus ochrogaster* were used, to avoid variations in activity due to the estrous cycle. All dyes selected for use in the field were tested on at least three animals in the activity wheel experiment.

Two types of experiments were used to determine the effect of the pellet implantation procedure on activity. A mock pellet implantation was performed on five animals. This consisted of making the small

opening in the skin, probing forward with forceps, and then closing the opening with a surgical clamp without placing any dye pellet subcutaneously. The second type of control was similar to the first except that inert beeswax pellets (the same size as the dye pellets) were placed under the skin of five prairie voles. These experiments were designed to determine the effect of the implantation operation on activity and the effect of the physical presence of a subcutaneous pellet on activity. The procedure for determining activity was the same for all the experimental animals.

FIELD

Missouri River Island

During a ten day period in December, 1959, a comparison was made of home range estimates obtained by live trapping methods and by the use of excreted dyes and dropping boards. The study was made on an island in the Missouri River, 18 miles southwest of Columbia, Missouri. Live traps of the type described by Blair (1941) were used. The trapping grid was composed of ten rows of ten traps each, spaced at 30 foot intervals. The grid covered an area of 2.06 acres. The plot was checked twice daily for five days; a total of 1,000 trap nights. Hamilton's (1937) scheme of toe clipping was used to mark the animals before release, after the initial capture.

An area covering about one-third of the trapping plot was found to have a rather high microtine population so the excreted dye home range study was conducted there. Dropping boards were placed at or near each former trap site, in a vole runway whenever possible. Boards were also placed at the halfway points of the 30 foot intervals in the trap grid, making the dropping board interval 15 feet. One hundred boards were used in the chosen portion of the trap quadrat. The dropping boards were made of ⅛ inch of ¼ inch thick masonite and were 4 inches square. White filter paper was affixed to the dropping boards with small pieces of cellophane tape at the corners. The white surface made possible the identification of colored urine spots. Initially some white-painted dropping boards were also included.

Specimens of *Microtus ochrogaster* which had been previously trapped in the recapture home range study were implanted with dye pellets on the sixth day of trapping. Five such animals were marked in the field using the same diameter and weight of pellet as in the laboratory. Each vole was released at its point of capture after recovery from anesthesia.

In some cases, two dyes resulted in urine of the same color. These dyes were still usable in the field if the urine spot from one or both changed color when a drop of acid or base solution was placed on it. For example, one vole was marked with safranin and another with superchrome violet; both color the urine red. The latter dye turns violet when a drop of 10 per cent potassium hydroxide is placed on a dyed urine spot, but the former stays red. Bottles of 10 per cent KOH and 10 per cent HCl were used in this dye pellet home range

test to conclusively identify urine spots which could have been from either one of two animals.

All live traps were closed after pellets were placed in voles, to prevent any limitation of the animals' normal movements due to recapture. Dropping boards were checked once each day over the five days following pellet implantation, for vole droppings and urine spots. Rodent droppings were noted and removed from the dropping boards at each visit to the grid. Boards with urine spots were replaced with clean ones. When the filter paper covers on dropping boards became dirty or stained from vegetation, they were replaced with clean boards.

Home range was calculated by the minimum area method from both sets of data. This method appeared to be the most valid, considering different grid intervals were used.

University of Missouri Entomology Farm

A second test comparing standard live trapping to the use of excreted dyes for home range determination of *Microtus ochrogaster* was made in a field on the University of Missouri Entomology Farm, ¼ mile southwest of Columbia, Missouri. A grid of 56 traps was placed at 25 foot intervals in a neglected pasture. The study took place over a 14 day period in late March and early April, 1960.

The same general methods used in the Missouri River island study were repeated in this test. The trapping grid was composed of seven rows of eight traps each and covered an area of about one acre. The traps were baited with pieces of apple because this bait was found to be quite useful in the spring for enticing microtines into traps. Peanut butter is of little value as a bait when new green vegetation is present. The plot was checked twice daily for seven days, a total of 1,400 trap nights. Traps were set in the most favorable location nearest each marked trap station in the grid.

An area covering about one-half of the trapping plot was found to have an adequate microtine population for excreted dye home range study. A dropping board interval of 12.5 feet was used, *i.e.,* boards were placed at trapping stations and also at halfway points. A total of 116 dropping boards were used in the chosen portion of the trap quadrat. White filter paper was affixed to all boards.

Specimens of *Microtus* which had previously been trapped at least four times were implanted with dye pellets after the seventh day of trapping. Six animals were marked in the field with pellets weighing 64-69 mg. Live traps were closed and the dropping boards were checked once each day for seven days. Vole droppings were removed and filter papers were replaced when necessary throughout the study period. Home range was calculated by the minimum area method for both live trapping and excreted dye data.

RESULTS

LABORATORY

The results from initial screening of 120 dyes and biological stains

for potential use in home range determination studies, eliminated many dyes from further consideration (Brown, 1960). Several dyes were eliminated because they killed the animal within a few days after implantation. Others colored the urine for a desirable period of time, but were rejected because the mice were obviously ill. Several dyes which colored the urine only 3-4 days were retested by increasing the amount of dye per pellet to two parts dye to one part beeswax. Doubling the concentration of dye per pellet had little effect in extending the period of urine coloration. Occasionally this increased dye concentration caused the animal to appear ill when the 1 dye: 1 beeswax weight pellet did not.

Eighteen dyes which showed promise in *M. musculus* were tested using *M. ochrogaster* in activity wheels (Brown, 1960). Most animals demonstrated considerable variation from day to day in the number of revolutions performed in the activity wheels. Depression of an individual due to a dye pellet was expressed by a marked reduction in wheel revolutions following implantation. The body weights of all animals in the activity wheels tended to decrease a few grams during the first seven days. This was probably because the animals expended more energy than they did in the holding cages. Most animals recovered a portion of this weight loss during the second week in the activity wheels regardless of the dye used or experimental manipulation.

Table I lists the nine dyes considered usable in home range determination and their color reactions. None of these dyes produced activity depression or other observable adverse effects under the test conditions. Acridine red and fluorescin are suggested as second choices because their colors are not as long-lasting as those of safranin-O and tropaolin-O respectively. Fluorescin can be separated from other orange-yellow dyes on the basis of fluorescence, but the field use of this was questionable.

TABLE I.—Dyes suitable for use in urine coloring experiments

Dye	Substitute dye	Excreted color	Color at acid pH	Color at basic pH
Safranin O	Acridine Red	Red-pink	Same	Same
Superchrome violet B		Red-pink	Same	Violet
Tropaolin O	Fluorescin	Orange-yellow	Same	Same
Meta cresol purple		Orange-yellow	Red-pink	Purple
Phenol red		Orange-yellow	Same	Red-pink
Methyl orange		Orange-yellow	Red-pink	Same
Fast green FCF		Green-blue	Same	Purple

Attempts were made to use fluorescin with other dyes; for example, to produce a fluorescent-safranin colored urine. Pellets were made from a 1 fluorescin: 1 dye: 1 beeswax mixture (by weight). Both colors were found to separate out when the urine colored by this type of pellet was placed on white filter paper. Fluorescin's color dominated the urine for the first 2-3 days after implantation; this then largely faded, and the other dye dominated the urine color the rest of the test period. Combining fluorescin with other dyes was therefore discarded because of variability in the urine color produced and the inconclusiveness of the fluorescence of colored urine spots.

The dyes listed in Table I fall into only three color groups, but dyes within each group are identified from one another by their colors in the acidic or basic pH range. Therefore seven different animals could be marked in the same area, and the dye in their urine spots identified with drops of acid and base solutions.

The sham implantations and the inert beeswax pellet implantations caused no depression of activity in *Microtus*. The simple implantation operation and the physical presence of a pellet under an animal's skin were thus eliminated as factors that prevent normal activity.

FIELD

Missouri River Island

A comparison of the number of records per animal using the excreted dye method and the live trapping method in a five day period is presented in Table II. The total number of colored urine spot records was slightly higher than the total number of trapping records for the five *Microtus*, but not significantly so. Table II also presents the minimum home range calculated in square feet from both sets of data, where such calculations could be made. The revealed home ranges using the excreted dye method were larger than the live trapping home range figures in the two cases calculated. Since the study period was only five days for each method, not enough

TABLE II.—Comparison of live trap and excreted dye home range determination for individual *Microtus ochrogaster*

Toe clip number	Sex	Dye	Number of trap records	Number of urine records	Live trap home range in sq. ft.	Excreted dye home range in sq. ft.
15	M	Safranin O	4	6	450	787.5
18	M	Meta Cresol Purple	3*	1	....	....
35	M	Superchrome Violet B	3	5	450	900
44	F	Fluorescin	2**	4	....	675
45	M	Phenol Red	1	0	....	....

* Captured in same trap.
** No home range calculation possible using minimum area method.

records for a more precise calculation of home range were obtained.

From 6 to 20 per cent of the dropping boards had droppings and/or urine spots on them each day the plot was checked. The lowest figure was noted following rainfall of .77 inches. The trapping success ranged from 27 to 36 per cent daily during the live trapping study on the part of the quadrat used for the excreted dye test.

Painted dropping boards were found to be inferior to filter paper covered ones, because when the urine evaporated, identification of the dye was nearly impossible on painted boards. Evaporation of urine on filter paper did not cause the dye color to fade or change. Rain washed the filter paper free of fluorescin spots, but did not affect safranin O, superchrome violet, or meta cresol purple. On the fourth day of the excreted dye test, 0.4 inch of snow fell, most of which melted upon contact with the moist vegetation. This light snowfall apparently did little to deter deposition of urine and droppings on the boards.

The filter paper on the dropping boards withstood weathering well during the five days. The paper did not become torn or detached from the boards even when wet. The paper on some boards had to be replaced during the period of rain and light snow when it was stained with brown drippings from dead vegetation.

University of Missouri Entomology Farm

Excreted dye home range determination is compared to live trapping home range determination in Table III. The number of trapping records were nearly twice as great as the total number of colored urine spot records for the six *Microtus ochrogaster*. Insufficient records were obtained from all but two animals to permit comparisons of the two methods. However, in all cases the sites recorded by the two methods were within short distance of each other.

Home range configurations using both methods tended to con-

TABLE III.—Comparison of live trap and excreted dye home range determination for *Microtus ochrogaster*

Toe clip number	Sex	Dye	Number of trap records	Number of urine records	Live trap home range in sq. ft.	Excreted dye home range in sq. ft.
12	M	Fast Green	10	8	937.5	937.5
13	M	Safranin O	7	7	312.5	468.8
14	F	Phenol Red	6	1	312.5	....
16	M	Superchrome Violet B	7	3	2187.5	234.4
22	M	Meta Cresol Purple	4	3*	312.5	....
23	F	Fluorescin	4	0	625.0	....

* Two records were at same station.

form rather closely in cases where sufficient records were realized. As Figure 1 demonstrates, excreted dye home range determination substantiates the validity of live trapping home range determination in voles. The home ranges of animals No. 12 and 13 show similar boundaries (with minor variations explained on the basis of difference in grid size) using both methods of determination.

From 2 to 8 per cent of the dropping boards had droppings and/or urine spots on them each day the plot was checked. There was no significant precipitation during the test period. The trapping success ranged from 5 to 30 per cent daily during the live trapping study of the part of the quadrate used for the excreted dye test.

DISCUSSION

Probably the most important factor determining the optimum weight and length of dye pellet to be used in an animal, is the total surface area of the pellet available for dye absorption. In general, a

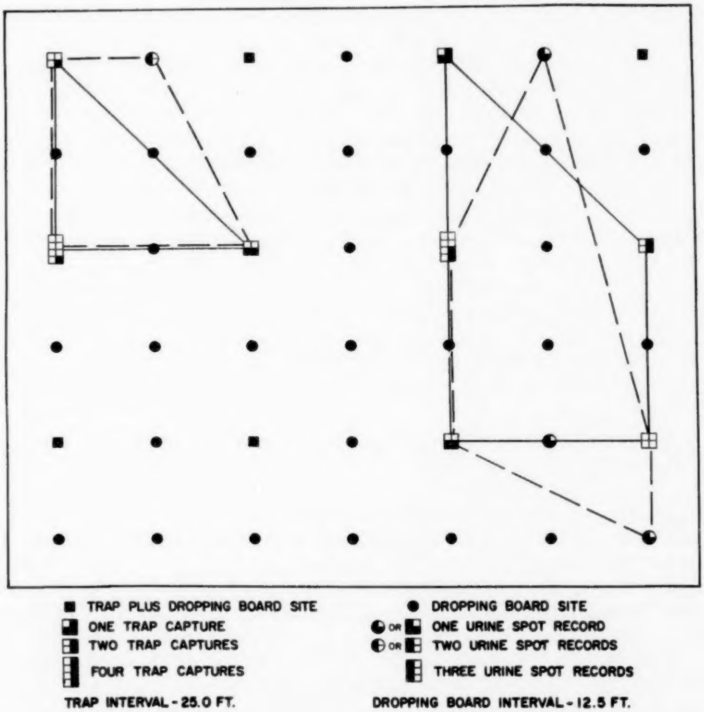

Fig. 1.—Comparison of the home ranges of two male *Microtus ochrogaster* when determined by the excreted dye and live trapping method.

pellet of twice the surface area of those recommended for use in *Microtus ochrogaster* was found to depress activity, and a pellet of half the surface area proved too small to color the urine long enough to be useful.

Further experiments with the group of dyes which were discarded because they failed to color the urine long enough, might extend the urine coloring period in some cases. Possible variations are (1) the use of different inert bases for the pellets, (2) increasing the concentration of dye per pellet, and (3) the use of pellets with a larger absorption surface.

None of the brown or black dyes screened was found to be satisfactory; testing more dyes of these colors might produce additional means of marking more animals. No really adequate blue-green dyes were realized from the screening experiments. Most of them colored the urine strongly, but depressed activity. Fast green was elected for final use because it did not depress activity, unfortunately it colors the urine only about four days. There is a possibility that further experiments with the blue-green range of dyes will provide a longer lasting substitute for fast green.

Incorporation of a radioactive isotope such as P32 into dye pellets would double the number of animals that could be marked in a given study area. For example, one animal could be implanted with a non-radioactive safranin O pellet and another with a radioactive safranin O pellet. A Geiger-Muller counter could then be used as Miller (1957) did, to distinguish the excretions of two such animals.

A method whereby fluorescin could successfully be used in combination with other dyes, and the excretion identified could probably be developed using simple photofluorometric methods. Photometric methods could also be used to identify two dyes that appear to be the same color and cannot be identified by the simple pH, color change method. Thus with refined techniques an impressive number of individual dyes, dye combinations, and dye-radioactive isotope combinations could be used to mark a large number of mammals on a study plot.

A number of advantages can be listed for the excreted dye method of home range determination over other methods. (1) Repeated handling of the animals is not necessary; they need to be live trapped only once. (2) In live trapping methods for home range determination, each animal spends a greater or lesser portion of its time confined in a trap, when it would normally be moving about its home range. This period of exposure and limitation of activity is avoided when the excreted dye home range method is applied. (3) Animals are not attracted to dropping boards by food as they are to baited live traps or the dye feeding stations of New (1958). (4) A large number of boards can be placed in a small interval grid (such that dropping boards occur every 5-15 feet) without disrupting the normal movements of small mammals. A grid of live traps placed at intervals approaching these distances would severely hamper the animals' move-

ments to the outer extent of their home ranges; each animal would probably be caught repeatedly in one or two traps. (5) The ability to use a small grid interval without disrupting movement, enhances the calculation of an accurate and meaningful home range. If a boundary strip is added to the minimum home range, it would be small and less likely to produce an erroneous home range figure that a larger one would. (6) Dropping boards need be checked only once a day under normal conditions, thus the animals are not continually disturbed by the observer as was the case in Godfrey's (1954) method utilizing radioactive leg bands and Kaye's (1960) method using gold-198 wires. (7) To some extent, each animal's range of movement in a 24-hour activity period is revealed.

A criticism of using excreted dyes is that the urine coloration does not last indefinitely. Also, it is possible, though not indicated in the field test, that male and female rodents are not equally inclined to use dropping boards. Although activity wheel results do not indicate it, a third criticism might be that the mechanical irritation of a pellet could cause increased activity or abandonment of the home range.

Since shrews and several small rodents in addition to *Microtus ochrogaster*, are known to utilize dropping boards (Emlen *et al.*, 1957), the home ranges of these mammals can be determined by the excreted dye method. In regard to the use of excreted dyes to mark animals when snow is present, it is possible that the method could be used on certain carnivores or even ungulates such as deer, once the proper pellet size is determined. Finally this technique might prove useful as a method for estimating population size in a modified Lincoln Index study (Lincoln, 1930).

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Patterns of Distribution of Sugar Maple, Acer saccharum Marsh., in Northern Cape Breton Island[1]

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ABSTRACT: An investigation has been made of the distribution patterns of *Acer saccharum* Marsh. on, and in close proximity to the limit of the range of the species in, northern Cape Breton Island. The limit of the range of the species cannot now be clearly delineated at sea level, but at greater elevations varies from altitudes of the order of 800 feet on seaward slopes to 1300 feet inland. In both primeval and second growth areas the density and dominance of the species vary widely, with a trend toward lower stocking with increasing altitudes. In some areas the limit of the range is marked by widely scattered trees whereas in others the density of the species is fairly high. Irrespective of stocking, there is no gradual transition in size toward a depauperate form or a marked decrease in vigour upon approaching the limit of the range of the species. On the basis of present evidence it is difficult to decide whether the limit of the range is stationary, advancing or retreating.

INTRODUCTION

Studies in the water economy of forest trees have been conducted in Nova Scotia for the past several years. In this program some attention has been given to species distribution patterns, and to patterns of morphological and physiological variation within species, with particular reference to sugar maple, *Acer saccharum* Marsh. This species constitutes extremely favorable material for investigations of this nature. In northern Cape Breton Island, the focal point of this work, sugar maple occurs over a very wide spectrum of sites, bounded on the one hand by rich bottomlands and on the other by a geographically well-defined complex of stations which marks the apparent limit of its range. Observations on the occurrence of sugar maple, with particular reference to conditions on the limit of the range of the species in northern Cape Breton, are presented in the following paragraphs. An empirical approach to the problem has been adopted, and in discussing the results speculation regarding causal relations has been avoided.

PHYSIOGRAPHY, SOILS, AND CLIMATE

The physiography of Cape Breton Island has been treated at length by Goldthwait (1924). Likewise Nichols (1918) has described in detail the topography of the northern reaches of the area. Similarly, Roland (1944) has included a brief but useful physiographic survey of the region in his flora. Consequently a very short review of the

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main features of the experimental area will serve the needs of the present discussion.

The bulk of northern Cape Breton Island comprises a massive plateau composed largely of Pre-Cambrian granites, syenites, quartzites, and slates. Goldthwait (1924) tentatively concludes that peneplanation of this upland surface was completed in the Cretaceous period, and that subsequently the entire region suffered a gentle upwarping. Several cycles of uplift and erosion and one or more glaciations are thought to have fashioned the contemporary morphology of the region.

From seaward the surface of the tableland is strikingly flat, although in actual fact the elevation ranges from 1200 to approximately 1800 feet above sea level. In some areas the plateau extends to the sea whereas in others a narrow coastal plain intervenes. The tableland is being dissected by a number of short, very swift rivers and streams, and in consequence is normally flanked, both on the coast and along the river valleys, by steep, tree-covered slopes. To the southwest and along the southern edge of the escarpment the approaches to the plateau remain steep, but the average elevation of the tableland is somewhat less.

In addition to the central mass of the plateau, there are several outlying regions of considerable area characterized by the same rock structure and type of surface, but with a somewhat lower average elevation. These outliers, together with the main body of the tableland, have probably been glaciated. However, our knowledge of the geography of the Pleistocene in northern Cape Breton Island is not extensive (Livingstone and Livingstone, 1958).

Slightly more than half of Cape Breton Island is occupied by lakes and lowlands. The latter are coincident with areas of soft sedimentary rocks of Carboniferous age (Goldthwait, 1924). Rolling hills of subdued outline seldom exceeding 500 feet in height are characteristic of the lowland regions.

Until recently there had been no extensive mapping of the soils of northern Cape Breton Island. However, the Experimental Farms Service of the Canada Department of Agriculture has recently completed a soils survey of the region, and the results are expected to appear in the near future. Several years ago the author made an examination of approximately 30 soil profiles located in hardwood areas in the northern reaches of the Island, and found a display of soil depths ranging from 12 inches on steep slopes to 4 feet in moist bottomlands. The soils of practically all sites examined were classified as sandy loams with an infrequent silt loam or loam.

Although meteorological observations are made at several locations in Cape Breton Island virtually no data are available regarding conditions encountered on the plateau. Useful summaries of data gained at coastal and inland observing stations may be found in publications of the Meteorological Division, Canada Dept. of Transport (1948), in Baughner and Thomas (1948) and Thomas (1953).

RANGE OF SUGAR MAPLE

There is considerable evidence to suggest that the northernmost reaches of Cape Breton Island are approximately coincident with the northern limit of the range of sugar maple. In recent years, despite considerable searching, Fernald (1911) was unable to collect the species in Newfoundland, the southern coast of which lies 30 sea miles north of Cape Breton Island. Likewise, in the eighth edition of Gray's Manual (Fernald, 1950), Newfoundland is not included within the range of sugar maple. Similarly, Rouleau (1956) does not include the species in his recent check list of the vascular plants of this province. The curators of the herbaria of the National Museum of Canada, the U.S. National Museum, and the New York Botanic Gardens, in answer to the author's inquiry, have replied that no specimens of *Acer saccharum* from Newfoundland are to be found in their respective collections. Other workers, including Hutchinson (1918) and Nichols (1918), indicate that this species does not extend into Newfoundland.

Perry (1931) and Erskine (1945) do not include *Acer saccharum* in the flora of St. Paul Island. It is noteworthy that the latter land mass is disposed only 10 sea miles to the northward of northernmost Cape Breton Island.

However, a contrary view with respect to the occurrence of sugar maple in Newfoundland has been expressed by several workers, including Bell (1897), Gleason (1952), Godman (1957), Harshberger (1911), and Little (1953). Likewise, Nichols (1935) appears to have reversed his opinion in a paper subsequent to that cited above.

METHODS AND RESULTS

Attempts by the author to delineate the northern limit of the range of sugar maple at sea level and at minor elevations in northernmost Cape Breton have been inconclusive. On the west coast of the Island, walking trips have been made as far north as Pollett Cove (Fig. 1) and the species observed consistently en route. On the east coast the species is common along the road between Capstick and Meat Cove. In the area of Cape St. Lawrence Light sugar maple has been found approximately one-half mile south of the coast at an elevation of the order of 320 feet. To the north of this station the area has been burned several times and individuals of the species have not been observed in the young birch-poplar-cherry association which is now found on the site. Similarly, in the area of Cape North — Money Point Light sugar maple has been found frequently along the trail to the lighthouse, the northernmost sighting being approximately one-half mile south of the Light at an elevation of 125-175 feet.

Elsewhere, however, the limit of the range of the species as affected jointly by latitude and altitude has been established fairly readily. To trace the distribution of the species the following procedure was adopted.

At or near the foot of each of a number of pre-selected routes to the plateau, a control point was established and its elevation determined. On three occasions advantage was taken of stations of known elevation established by the Geodetic Survey of Canada. In the course of the ensuing ascent, wet and dry bulb thermometer and atmospheric pressure readings were made at intervals of 10 minutes at the bench mark. Following stabilization and comparison of instruments at the datum, a climbing party equipped with two aneroid barometers and a sling psychrometer moved upwards from the datum along a predetermined mean line of advance recording temperature and pressure at 10 minute intervals synchronously with readings being taken at the datum. However, at higher elevations, upon approach-

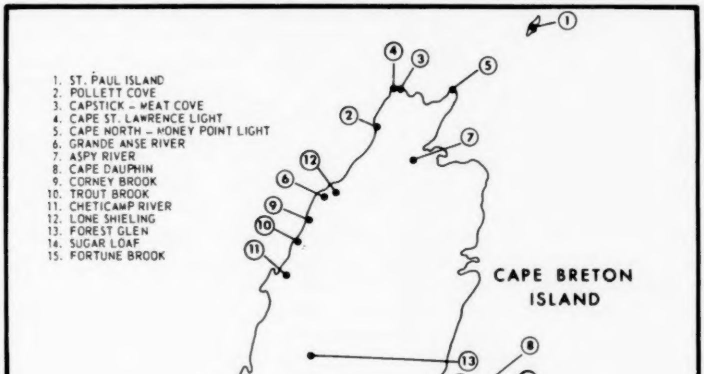

Fig. 1.—Map of Cape Breton Island.

ing the altitudinal limit of the range of sugar maple, the progress of the party was directed from sample tree to sample tree with readings taken as requisite without reference to a time interval. Upon establishing the apparent altitudinal limit of the species, temperature and pressure measurements were made at several trees, and the climbing party next continued forward a distance of 10 to 20 chains with readings being taken at frequent intervals. An offset of varying length at right angles to the mean line of advance was then made, and the climbing party next moved down into the range of the species along a reciprocal course. Upon regaining contact with individual sugar maple trees the apparent limit of the range was again delineated, time, temperature, and pressure measurements being made at a number of trees.

As noted above, at the commencement of each climb, barometers were left to become stabilized at the datum point and then read. Wet and dry bulb temperatures were recorded simultaneously. Pressure and temperature trends were subsequently followed closely at the datum during the ascent. At the conclusion of the operation, all instruments were read again at the bench mark following stabilization. With sufficient justification, as judged by the observed barometric tendency at the datum during the course of the climb, a straight line or otherwise was drawn connecting the initial and final datum readings of the instruments accompanying the climbing party. Intermediate control values, in time, were taken from the resulting graphs. To minimize the possibility of interpretative errors in pressure readings, ascents were made only under favorable weather conditions. A further means of control was achieved through the plotting of surface analysis charts which yielded information regarding the synoptic picture. Elevations were determined with the aid of the following formula (Brunt, 1952).

TABLE I.—Elevation of limit of range of sugar maple at various locations in Cape Breton Island

Position	Transect	Location	Exposure	Elevation at limit (ft.)
Cape Dauphin	A	Coastal	SE	810
Corney Brook	B	Coastal	W	720
Trout Brook	C	Coastal	NE	785
Cheticamp River	D	Slightly inland	N	782
Aspy River	E	Slightly inland	SE	1355
Lone Shieling	F	Slightly inland	NE	1120
Forest Glen	G	Inland	E	1359
Sugar Loaf	H	Inland	SE	1338
Fortune Brook	I	Inland	SW	1247

$Z = 221\ T\ (\log p_0 - \log p)$ where
$Z =$ height of station in feet above datum
$T =$ average of temperature readings at bench mark and at observing station in degrees Absolute
$p_0 =$ pressure in millibars at datum at time t
$p =$ pressure in millibars at observing station at time t

Results gained in a number of climbs to the plateau are included in Table I.

Distributional patterns in sugar maple were traced by means of transects extending from bottomlands to the upper reaches of the plateau and oriented as requisite. Along these transects all trees 3 inches and above in diameter, and located within one-quarter chain of the center line were tallied.

Stand and stocking relations were investigated through the medium of 0.2 acre plots established in a wide variety of sites. Within plots all trees 3 inches and above in diameter at breast height were tallied by species, crown class, and condition, and by azimuth and distance from a central point, the center of the plot. Sample trees were felled at the plots, and later used for purposes of analysis and for morphological and histological examination.

TABLE II.—Structure of lowland, second growth, hardwood stands in northern Cape Breton Island

	Plot No. 1		Plot No. 2		Plot No. 3	
D.B.H.	Sugar maple	All species	Sugar maple	All species	Sugar maple	All species
3	4	7	..	..	..	1
4	14	18	4	6	6	11
5	6	6	7	6	7	11
6	10	10	6	6	10	12
7	7	7	12	17	9	10
8	5	5	7	8	4	4
9	1	1	12	15	6	7
10	4	5	7	11	7	7
11	4	5	7	9	11	11
12	1	1	..	..	5	5
13	3	3	1	3	1	1
14	..	..	..	3	3	3
15	1	2			1	1
16	3	4			1	1
17	..	..			1	1
18	..	..				
19	..	..				
20	..	1				
Age (yrs.)	65	..	90		110	
No. of trees per acre	315	375	310	425	360	420
Basal area per acre (sq. ft.)	115	144	113	172	166	173

DISTRIBUTIONAL PATTERNS — LOWER, MIDDLE, AND UPPER SLOPE STANDS

The percentage of sugar maple in second growth bottomland stands in northern Cape Breton Island ranges from low to very high, with almost pure stands of the species frequently being encountered. Density is high and growth in height is frequently good. The structure of several such stands is outlined in Table II.

In second growth areas, in passing upward toward the surface of the plateau, some variation in form and considerable fluctuation in the density and dominance of sugar maple are encountered. Frequently, therefore, the distinctly sugar maple characteristic of the forest, so clearly evident in bottomland sites, is lost.

Stand and stocking relations in old growth bottomland stands may be investigated at a few localities in northern Cape Breton Island. In these stands density apparently is normal, and the percentage of sugar maple varies widely. Basal area in better stands reaches 230 sq. ft. per acre, with sugar maple occasionally constituting 95 per cent of this figure.

TABLE III.—Percentage composition in transects in second growth and primeval forests in northern Cape Breton Island
Transect No. 1 (second growth)

Dist. from datum (chains)	No. of trees/acre		Basal area/acre (sq. ft.)	
	Sugar maple	All species	Sugar maple	All species
1	60	400	9	87
3	..	140	..	85
5	..	180	..	61
7	..	220	..	104
9	20	260	2	54
11	20	260	4	72
13	120	300	29	65
15	100	180	34	69
17	160	260	100	103
19	220	300	118	162
21	60	140	11	74
23	40	200	45	79
25	120	200	88	99
27	180	300	94	146
29	120	240	59	102
31	60	340	29	126
33	..	180	..	81
35	..	300	..	57
37				
39				
41				
43				
45				
47				
49				

Transect No. 2 (second growth)

Dist. from datum (chains)	No. of trees/acre		Basal area/acre (sq. ft.)	
	Sugar maple	All species	Sugar maple	All species
1	180	380	83	147
3	140	340	28	106
5	80	260	14	61
7	110	120	25	29
9	200	260	43	67
11	..	420	..	117
13	60	220	6	46
15	160	300	43	72
17	80	280	18	87
19	120	360	21	50
21	80	240	48	101
23	60	220	37	132
25	60	200	43	89
27	120	140	57	61
29	20	40	16	20
31	140	140	103	103
33	40	40	9	9
35	..	80	..	85
37	..	140	..	93
39	..	120	..	64
41	..	120	..	56
43	..	20	..	3
45	..	160	..	90
47	..	200	..	93

Transect No. 3 (Primeval)

Dist. from datum (chains)*	No. of trees/acre		Basal area/acre (sq. ft.)	
	Sugar maple	All species	Sugar maple	All species
1	80	120	28	84
3	120	180	45	107
5	140	180	97	11[illegible]
7	180	180	186	186
9	160	160	144	144
11	80	80	128	128
13	160	240	27	108
15	100	200	44	142
17	60	120	40	52
19	160	200	49	103
21	160	180	112	148
23	80	180	43	106
25	60	240	32	136
27	20	180	5	72
29	..	220	..	62
31	..	500	..	95
33	..	120	..	73
35	..	40	..	14
37	..	180	..	37
39	..	20	..	9

* No trees 3 inches or more in diameter were encountered at 41 to 49 chains from datum.

Despite the proximity of the examination area to the apparent northern limit of the range of sugar maple, individuals exceeding 100 feet in height and 30 to 35 inches in DBH, though not common, occur in the valley of the Grande Anse River. In second growth stands of good quality co-dominant trees frequently reach heights of 60 feet in 50 years.

Passing upward toward the surface of the plateau in old growth, undisturbed areas, the density and dominance (basal area) of sugar maple vary considerably, but the distinctly sugar maple characteristic of primeval bottomland stands is sometimes retained, particularly at lower and middle elevations. Data gained in transects from bottomland sites to the limit of the range of the species in second growth and primeval stands are summarized in Table III.

Irrespective of conditions obtaining in nearby bottomlands, many hardwood areas on the upper flanks of the plateau have not been logged. However, the history of these stands may differ widely, and the age class distribution pattern is complicated. Despite the age of many of these trees (200 years), the height of the average co-dominant is not great, seldom exceeding 45 feet, with a diameter at breast height of less than 14 inches. In these upper level stands the percentage of sugar maple is frequently high and the density of stocking is usually normal (Table IV).

Sugar maple trees in stands in southern and central Cape Breton Island located on the surface of the plateau but growing at elevations below the altitudinal limit of the species are commonly short and of poor form, and the density of the species is commonly low.

DISTRIBUTIONAL PATTERNS — RANGE LIMIT STANDS

Topographic conditions obtaining at the limit of the range of sugar maple, together with stand and stocking relations vary widely. Along the seaward approaches to the plateau the limit of the range of the species occurs at elevations of the order of 800 feet, that is, on the middle and lower flanks of the escarpment. As noted previously, upon passing upward toward the surface of the plateau the density of sugar maple is variable and frequently low, particularly in second growth stands, and on seaward slopes the limit of the range is delineated by scattered and well separated trees. In an altitudinal sense, however, the limit is abrupt. There is no gradual transition in size toward a depauperate form, or a marked decrease in vigor upon approaching the limit. On the contrary the individual sugar maple stems on the periphery of the range are commonly co-dominants comparable in size to other trees in the overstorey.

Conditions at the limit of the range in old growth stands were investigated on the steep sides of the valleys of the Grande Anse and Aspy Rivers. Here the altitudinal limit is of the order of 1250 feet, that is, on the upper reaches of the flanks of the plateau. In some sections of this area co-dominant, scattered trees mark the limit of the range. Reproduction of sugar maple is scanty and confined to

the immediate vicinity of seed bearing co-dominants. In topographically difficult areas, the density of sugar maple may be very low and the limit of the range consequently poorly defined. In one case, on an extremely steep and exposed southeasterly slope above the Aspy River, characterized by a very unthrifty growth of hardwoods not forming a closed stand, the limit of the range of the species is marked by seedlings growing well above the "furthest on" position of the scattered members of the overstorey.

TABLE IV.—Structure of upland, hardwood stands in northern Cape Breton Island

	Plot No. 4		Plot No. 5		Plot No. 6	
D.B.H.	Sugar maple	All species	Sugar maple	All species	Sugar maple	All species
3	2	3	1	2	1	2
4	2	2	1	2	..	12
5	..	1	1	2	1	7
6	2	2	2	2	..	5
7	2	2	..	2	1	4
8	1	2	4	4	..	4
9	1	2	5	5	1	5
10	4	4	1	2	1	3
11	7	10	1	2	1	4
12	2	2	..	..	1	3
13	1	1	1	2	..	..
14	1	1	1	1	..	4
15	..	..	..	3	..	2
16	..	..	..	..	..	1
17	1	2	..	1	..	..
18			..	..	..	..
19			..	2	..	..
20			..	1	..	..
21			..	..	..	1
22			..	1	..	..
23			..	1	..	1
24			..	..		
25			..	..		
..						
..						
48			..	1		
Age (yrs.)	110		160		110	
No. of trees per acre	130	175	90	180	35	290
Basal area per acre (sq. ft.)	70	102	37	199	14	139

At inland stations a rather different situation obtains. Here the limit of the range is found on the more leisurely slopes of the upper reaches of the plateau. Under these circumstances sugar maple occurs not as widely-separated, individual trees but usually in mixed-wood stands (Table IV). Again, individuals on the limit are co-dominant, usually thrifty trees. Reproduction of the species is scanty and occurs in close proximity to seed-bearing members of the overstorey.

Preliminary observations indicate that germinable seed is produced in quantity on the limit of the range, but reproduction is scanty, with seedlings distributed in close proximity to the seed-bearing members of the overstorey. At present there is no suggestion of a wide age class distribution in seedlings. Rather, the size and occurrence of reproduction serves to maintain the abruptness of the limit of the range of the species.

Stand characteristics frequently are best considered within the framework of the technical forester's yield table, and this practice has been adopted in the present instance. We have been extremely fortunate in this regard in that Mr. S. J. Kostjukovits of the Department of Lands and Forests, Province of Nova Scotia, has most generously made available to us his unpublished compilations of growth and yield in hardwoods in the Province. In the present study appeal has been made also to the data of Gevorkiantz and Duerr (1937) and

TABLE V.—Stand and stocking relations in hardwood forests in northern Cape Breton Island

Plot	Location	Age	Ht. of av. Co-dom. tree	Trees per acre	Basal area (sq. ft./-acre)	Site-quality (A)[1]	(B)[2]
A	Bottom-land	65	66	375	142	2	1
B	Upland	190	42	245	144	5	3
C	Lower slopes	85	64	385	151	3	2
D	Upland	160	43	180	199	5	1
E	Upland (limit of range)	110	46	290	139	5	3
G	Upland	110	39	175	102	5	5
I	Upland	90	43	340	153	5	2
J	Upland	90	43	340	128	5	3
K	Lower slopes	90	72	425	172	3	1
L	Bottom-land	110	64	420	173	4	1
N	Upland (limit of range)	85	45	210	150	5	2

[1] Based on height-age relations.

[2] Based on basal area per acre.

Hawes and Chandler (1914). A synthesis of observations made in a number of plots on a variety of sites is presented in Table V.

DISCUSSION

Reference to Table V indicates that site determination based on height-age relations leads to the inclusion of all upland plots in sites of poor quality (sites 4 and 5). On the contrary, a classification based on age, density, and dominance (basal area) results in the assignment of much superior site quality values. Clearly the height of the average co-dominant trees on upland sites in Cape Breton deviates markedly from normal. Possibly wind is involved here.[2]

Perhaps the most striking feature of the results gained in the present study is the demonstration of the abrupt nature of the "line" which marks the limit of the range of sugar maple in Cape Breton Island. Almost invariably the limiting trees are co-dominant members of the stand, approaching or equalling, both in height and diameter, the dimensions of trees of other species represented in the overstorey. This situation obtains on all types of topography, although the actual elevation of the limit and the degree of slope may vary widely. Similarly, as noted previously, the density and dominance of sugar maple on the limit of the range varies considerably.

In areas of uniform terrain, for example interfluves on the more leisurely upper slopes of the plateau at inland locations, there is not an uncommonly wide change in azimuth from tree to tree along the limit. However, topographic features deriving from any cause, and particularly water courses and exposed ridges, may be marked by considerable differences in the elevation of the limit, and by pronounced changes in form and stocking.

Wulff (1950) and Braun (1950) indicate that the range of a species is limited by the interrelations of a complex of factors, and their view is rather well supported by circumstances attending the limit of the range of sugar maple in Cape Breton Island. It is very difficult to demonstrate coincidences between the limit of the range of sugar maple and individual soil and associated topographic factors. In this regard it is of interest to recall the homogeneous nature of the rocks from which the soils of the region have been derived.

The situation is ostensibly the same with respect to meteorological considerations (see also Dansereau, 1957 in this regard). However, marked changes in the size, form and habit of individual stems in

[2] In this regard it is of interest to note that an analysis of storm track data presented in the Monthly Weather Review of the United States Weather Bureau indicates that in the interval 1939-1959 inclusive, approximately 2455 cyclonic centers moved across longitude 61° W., north of latitude 20° N. Of this total 2080 centers (85%) passed across the above meridian between latitude 30° N. and 60° N. The average latitude of passage of the centers across the meridian of 61° W. was 47° N. Further information bearing on the frequency and intensity of storms in the region of Cape Breton Island may be found in Volume One of the United States Navy's "Marine Atlas of the World."

bottomlands and at higher elevations point strongly to the possibilities of a climatic influence. Similarly, the wide differences in the elevation of the limit of the species on seaward versus inland slopes constitute presumptive evidence that meteorological factors are of significance in the distributional pattern of the species in Cape Breton Island.

The forests of Cape Breton, with the possible exception of the pure fir stands of the upland, have been included within the hemlock, white pine, northern hardwoods association of Nichols (1935); see also Braun (1950). In Braun's view, the vegetation of the hemlock-white pine-northern hardwoods region derives from post-Wisconsin migrations "which brought about an expansion from the unglaciated Allegheny Plateau and northern Allegheny Mountains without pronounced modification of type. The climax elements are almost entirely a result of these expanding migrations." Several species attain the limit of their ranges within this region, and Braun suggests that with further development of topography and soils, maple, beech, and hemlock may move farther north.

It is difficult on the basis of present evidence to decide whether the limit of the range of sugar maple in northern Cape Breton is now stationary, advancing, or retreating. Application of the criteria of Griggs (1946) regarding advancing timber lines leads to inconclusive results. Likewise, age class distribution patterns in reproduction and overstorey do not suggest any particular trend.

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Interaction of Natality, Mortality and Movement during One Annual Cycle in a Microtus Population

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ABSTRACT: A population of meadow mice, *Microtus pennsylvanicus*, was studied through one annual cycle, near East Lansing, Michigan. In May the mice were at a very low density and living under good conditions of food and cover and experiencing little competition. Because of high natality the population increased rapidly throughout the summer and fall. Breeding ceased in January, and the population continued to increase in February as a result of immigration. Mortality was highest in the summer and least in the winter. This was the result of (1) change in the age composition of the population, and (2) probable reduction of predation due to a persistent snow cover. A life table showed that mortality was highest in the postnestling juveniles and young adults. In other age classes mortality continued at approximately 50 per cent. The natural rate of increase of the population was -0.0315 daughters per female per day. Although the rate of increase was negative, immigration was sufficient to cause the population to increase in size.

Although the population dynamics of meadow mice of the genus *Microtus* has been the subject of considerable research both in North America and Europe, our knowledge of the interaction of mortality, natality, and movement in a single population of this genus is still far from complete. In this paper I intend to present a detailed analysis of these factors in a population of *Microtus pennsylvanicus*. The data for this analysis were obtained during an intensive one and one-half year investigation of the energy flow through an old-field vegetation — *Microtus pennsylvanicus* — *Mustela rixosa* food chain. (Golley, 1960).

My studies were made in 1956 and 1957 in an abandoned field near the Michigan State University campus, East Lansing, Michigan. Blue grass (*Poa compressa*), wild carrot (*Dauca carota*) and Canada thistle (*Cirsium arvense*) were the chief dominants in the vegetation. Since occasional burning was the only disturbance to the vegetation for about 15 years prior to the study, a dense sod of grasses and perennial herbs had developed and provided an abundance of cover and food for the meadow mice. During the study period the weather was unusually mild. The temperature was above average in every month except September, 1956, and January, 1957, and precipitation was below average throughout the fall and winter. The study area was surrounded on four sides by orchards, alfalfa fields, and old-field vegetation, all of which furnished habitat for *Microtus*.

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METHODS

Population density, natality, and mortality were determined by a mark and recapture technique using a modified Sherman live-trap, with a wooden floor and hardware cloth end-wall and door. Mortality of mice within the traps was kept at a low level by covering the traps with aluminum foil-covered-asphalt shingles. The traps were baited with oatmeal. The trapping pattern was devised by Hayne (1959) and is described in Golley (1960). Briefly, the pattern consisted of two cross lines 100 meters in length, of 50 traps each. These lines were operated alternately for 24 hours, for a total of 6 days, resulting in three days of trapping for each line. The ratio, number of individuals captured in common by both lines divided by the average capture per line, provided an estimate of the fraction the average capture per line was of the total population. This technique was tested in an isolated field by Hayne and Golley (unpublished) by using the cross-line trapping pattern to provide a population estimate and then checking the estimate by removing all the mice in the area with snap traps. The population estimated obtained by the two methods were nearly the same (217 and 225 per acre).

Each newly captured animal was marked by toe clipping, and weighed, sexed, and examined for reproductive condition. Pregnancy was determined by palpation of the abdomen. On subsequent captures the animal was weighed and again examined for pregnancy. The age of the specimens was determined by converting live weight to age in days, using Hamilton's (1937) growth curves for *Microtus pennsylvanicus*. Although Whitmoyer (1957), in a study of growth rate of laboratory-raised *Microtus pennsylvanicus*, concluded that weight was only a general criterion of age, the age-weight conversion is used here for lack of a more exact field criterion.

Natality was determined from knowledge of the percentage of females found to be pregnant, the known gestation period for the species (21 days) and the average litter size in snap-trapped specimens taken in similar habitat at the same time of the year (5 young per litter). The number of days for an average female in the population to give birth to a litter was estimated by dividing the gestation period by the per cent pregnancy (termed f). Every $21/f$ days an average female would produce a litter of 5 young, of which 2.5 were females. Thus in the time interval, $21/f$ days, one female would increase to 3.5 females. With this information the following formula was used to calculate natality:

$$\frac{\log_e 3.5}{\frac{21}{f}} \times t \times p \qquad 1.$$

where f is the per cent pregnant females, t is the time interval between trapping periods, and p is the mean population.

Mortality equalled the disappearance of individual mice from one period to another, assuming that all the animals in contact with the line were captured at each period. This assumption is nearly correct since only 14 of approximately 500 mice were not taken in every consecutive trapping period from the first to the final period in which they were captured. For any one trapping period, only 10 per cent of the new captures were made in the last two days of trapping; this is further indication that the 6 days was adequate to capture the population in contact with the lines.

Although, the cross-line trapping pattern could not be used to estimate the home range of the mice, an index of movement could be calculated by averaging the distances each animal moved between captures in one trapping period, assuming a straight-line movement from one trap to the next. This index of movement does not tell how far an animal actually moved, but is an indication of the movement activity of the animals during a trapping period.

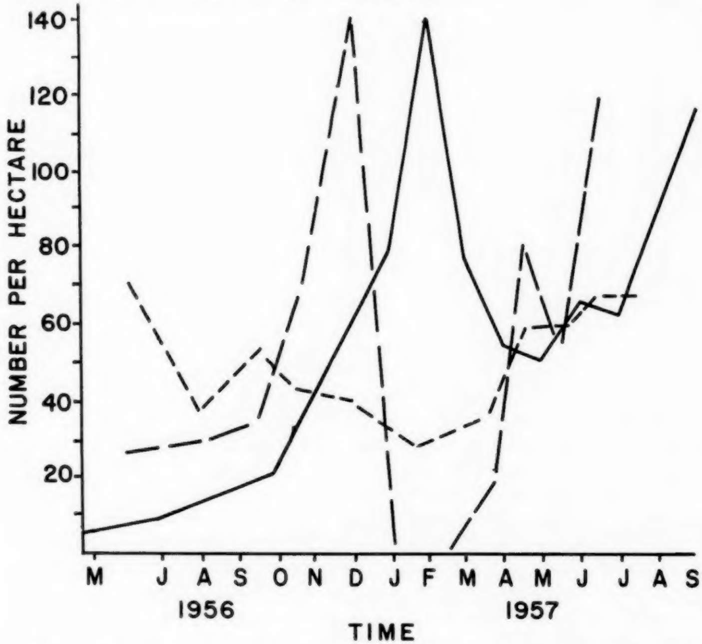

Fig. 1.—Density (solid line), natality (long dash line) and mortality (short dash line) of *Microtus* during 1956 and 1957 in southern Michigan. Natality and mortality are shown as the number of births or deaths per hectare per month.

RESULTS

At the beginning of the investigation practically no animals were present on the study area. The population exhibited an extremely rapid rate of increase (Fig. 1) during the first summer and fall, the rate being almost a doubling of the population every two months. This increase did not continue throughout the year. A reduction in the population occurred in mid-winter, and a second increase began the following spring.

Birth of mice per hectare per month (Fig. 1) increased throughout the spring and summer to a peak in December. Breeding stopped during winter; pregnant females were not found in January, or February, and the pregnancy rate was low in March (11%). Hamilton (1941) also found that *Microtus pennsylvanicus* in New York stopped breeding during the winter, except when the population density was extremely high.

Mortality trends (Fig. 1) were somewhat different than those expected. It was anticipated that in the winter cold rains and heavy snow-fall might cause greater mortality in the population, but this does not appear to have been the case. As shown in Fig. 1, mortality was highest during the summer and decreased to a low in mid-winter. The average mortality for each age-class was considered in a life table (Table I). Highest mortality (61% and 58%) occurred in the post-nestling juveniles (11 to 20 grams) and young adults (21 to 30 grams). In other age groups mortality was about 50 per cent.

Since the population of *Microtus pennsylvanicus* was living under near optimum conditions, the natural rate of increase of the population *(r)* might be expected to approach the innate capacity for increase of the species. The innate capacity for increase, as defined by Andrewartha and Birch (1954), is the maximal rate of increase when quantity of food, space, and other animals of the same kind are kept at the optimum. Following the methods of Birch (1948), a female life table and age specific fecundity table were prepared (Table II). This fecundity table is age specific because the pregnancy rate does vary with age; however, the number of young per litter which might be

Table I.—Life table for the population of male and female *Microtus pennsylvanicus*

Weight Class x	Days	No. surv. at beginning of age period of 100 l_x	No. dying in interval d_x	Mortality rate/100 $100q_x$	Expectation of life e_x
0-10	0-10	100.0	50.0	50.0	11.4
11-20	11-21	50.0	30.5	61.0	15.2
21-30	22-33	19.5	11.3	58.0	19.5
31-40	34-54	8.2	4.3	52.5	27.0
41-50	54-103	3.9	2.1	53.9	31.8
51+	104+	1.8	1.8	100.0	12.8

Table II.—Life table and age specific fecundity table for female *Microtus*

Midpoint of age-class days x	Days between age-periods t	Total no. ♀	No. surv. to next period	Prob. of ♀ being alive at beginning of period l_x	% pregnant	$\frac{21^1}{f}$	$\left(\frac{\frac{\text{nat. log. } 3.5}{21}}{f}\right)$ m_x	t $l_x m_x$	$x m_x l_x$
5.0	—	2	1	1.000	0.00	—	.0000		
16.0	11	50	14	.500	.21	100.0	.1378	.0689	1.1024
27.5	12	103	73	.140	.54	38.9	.3865	.0541	1.4880
44.0	21	73	21	.099	.59	35.5	.7411	.0734	3.2283
79.0	49	17	6	.029	.80	26.2	2.3430	.0649	5.3681
104.0	—	1	1	.010	0.00		.0000		
							$R_o =$	.2643	11.1868

$$T = \frac{11.1868}{.2643} = 42.33 \text{ days} \qquad r = \frac{-1.3318}{42.33} = -0.0315$$

[1] Gestation period/percent pregnancy.

age specific is held constant at 5. The net reproductive rate (R_o) indicated that this population would multiply 0.264 times per generation. The mean generation time was approximated by the formula:

$$T = \frac{xl_xm_x}{l_xm_x} \qquad 2.$$

where T is the mean generation time, and x, l_x, and m_x are taken from the female life table. The mean generation time was 42.33 days. With this information the natural rate of increase (r) was estimated as:

$$r = \frac{\log_e R_o}{T} = \frac{\log_e 0.2643}{42.33} = -0.0315 \text{ daughters}/♀/\text{day} \qquad 3.$$

This means that at any instant the death rate is greater than the birth rate.

The movement index (Table III) showed some interesting fluctuations. Although males and females appear to have approximately the same average movement index when the entire year is considered, during the spring and summer the males show greater movement than the females. The females when relieved of maternal duties during the winter move about more than the males. Total movement during the winter for both males and females was less than during other seasons.

DISCUSSION

The aim of this report is to explain the observed changes in numbers of meadow mice by considering the interaction of natality, mortality and movement. Natality increased during the spring, summer and fall, until January when all reproductive activity ceased. The reason for a winter cessation of breeding in *Microtus* is not completely known. Baker and Ranson (1932) showed that *Microtus agrestis* required a light ration of 15 hours light per day to breed in the labora-

TABLE III.—Seasonal movement and mortality of male and female *Microtus*

Average Movement in Meters			
Season	♂	♀	Both Sexes
September to December	16.5	16.1	16.2
January to March	8.3	16.0	9.1
April to June	12.9	9.7	11.4
July to September	17.7	9.1	14.3
Average	13.5	13.1	12.8
Average Per Cent Mortality Per Month			
Season	♂	♀	Both Sexes
September to December	51	39	47
January to March	28	38	31
April to June	61	65	64
July to September	67	56	64
Average	47	48	47

tory. Whitmoyer (1957) also observed this to be true for *Microtus pennsylvanicus*. However, in this field study there appears to be only slight correspondence between breeding and light, when light is represented by the hours of sunshine recorded by the East Lansing weather station and hours of light between sunrise and sunset, taken from the Tide Tables, 1957-1958. Natality reached a peak in December (Fig. 1) which was the period of minimum light. Since Hamilton (1941) reported winter breeding during high population densities, probably factors other than light are also important in regulating breeding in this species.

Reduction in mouse density during the winter was due to the cessation of breeding associated with a continuing mortality. However, mortality was lower in winter than during the spring or summer (Table III). Probably this depression of winter mortality rates was largely due to a change in the age composition of the population. As shown in the population life table (Table I), the mortality rate was highest for the 11 to 20 gram weight class. Since these animals and the nestling young were not present in the winter population, the mortality would be less than when these ages were present. The oldest mice also decreased during the winter period, with the result that the late winter population was made up mainly of 21 to 40 gram animals.

Reduction of predation, especially avian predation, due to persistent snow cover may also have contributed to low winter mortality rates; however, quantitative data on this point are not available. Snow was on the ground for 28 days in January and 23 days in February, 1957 (East Lansing Weather Bureau, Local Climatological Data). Although, *Microtus* dug through and ran for short distances on top of the crust, a myriad of tunnels and runways were concealed beneath the snow. No signs of avian predation on *Microtus* were noted during the winter period.

There appears to be a correspondence between the amount of movement (as indicated by the movement index) and mortality in both sexes (Table III), especially in winter when movement and mortality both decrease. Although this correspondence is not unreasonable, since the probability of having an accident or of contacting a predator might be expected to be greater as the animals move about more, the correlation of movement on mortality for both sexes is not significant ($r = 0.089$). Movement may be an influence on mortality, but other factors seem more important in this particular situation.

Increase in the population during the spring and summer was due to production of new mice by the resident population. In January, when there was no reproductive activity, the population continued to increase and reached a peak of about 140 mice per hectare. This late season increase resulted from immigration of mice into the study area. The study area was located in optimum habitat and mice living on the adjacent exposed hillsides where the vegetation was less dense apparently moved into the dense lowland sward of grasses and herbs.

Throughout January and February there was an increase in capture of unmarked mice immediately before or during snow storms associated with an increase in the incidence of capture of the resident mice. This increase was interpreted to mean that the mice in some way anticipated storms and moved into more favorable habitat for the storm period and possibly for the entire winter.

The negative rate of natural increase (Table II) may also be explained by the immigration of mice into the population. The life table was calculated from all mice appearing in the population throughout the year, and included immigrant mice which did not reproduce while in the population. The increase in numbers of mice over the year is the result of both natality and immigration. Although the death rate at any instant was larger than the birth rate, immigration was sufficient to cause the population to increase in size.

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Responses of Small Mammals to Live-traps and Weather Conditions

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ABSTRACT: A comparison was made between the responses to live-traps of marked and unmarked individuals of *Microtus pennsylvanicus* and *Peromyscus leucopus*. Previously captured individuals of *M. pennsylvanicus* were more readily captured than were the unmarked ones, even after an interval of a month. There was no difference in the rates of capture of marked and unmarked *P. leucopus*. Comparisons of a given live-trapping technique utilized in two different habitats (marsh and old field) indicated no significant difference in its effectiveness after the second day of trapping. *M. pennsylvanicus*, in an old field, was found to abandon diurnal activity in favor of nocturnal and/or crepuscular activity when the temperature rose above 20° C. During the winter, when the temperature dropped below 0° C, activity was much less at all times. Except for less activity during the days the temperature rose above 20° C, such responses were not observed in the marsh. *Blarina brevicauda* was found to be more active on cloudy days than on those that were sunny or rainy. No correlations between activity and temperature variations was observed for this species.

Estimates of population densities of small mammals are normally derived from trapping data. The results depend upon a variety of factors in addition to the actual abundance of the mammals. Variations in responses to traps, positioning of the traps, home range size, amount of movement within the population, and weather conditions influence the estimates of population densities (Sealander and James, 1958; Goodnight and Koestner, 1942; Hayne, 1950; Calhoun and Casby, 1958; Getz, 1961a).

Responses to traps are particularly important. A method widely used in determining population densities from trapping data is the proportional method ("Lincoln Index" or modifications thereof; Hayne, 1949). A basic assumption involved in this method is that the probability of capture of the marked animals is the same as that of the unmarked animals. Morris (1955) and Chitty and Kempson (1949) found that marked individuals entered traps more readily than did those that had not been captured previously. Tanaka (1956) found the same to be true of certain species, while in others the probability of capture decreased after the initial capture. He further found that some may be "isoresponsive." Leslie (1952) assumed the marked and unmarked individuals to be captured with equal facility, although prebaiting was utilized to overcome any initial reluctance of individuals to enter traps (this initial reluctance has been discussed by Sealander, *et al.*, 1958).

Responses to weather conditions also influence estimates of population densities, particularly those sampled by means of snap-back traps. Burt (1940), Gentry and Odum (1957), Pearson (1959, 1960)

and Benton (1955) have discussed the responses of small mammals to weather conditions. There is still much to be learned, however, concerning the influence of weather upon the activity of small mammals.

The present paper deals with the meadow vole, *Microtus pennsylvanicus,* the white-footed mouse, *Peromyscus leucopus,* and the shorttail shrew, *Blarina brevicauda.* The data concerning *Microtus* and *Blarina* were compiled from a study of small mammal distributions in southern Michigan (Getz, 1959); those pertaining to *Peromyscus* were taken from Burt's study of small mammal populations on the Edwin S. George Reserve, 1935 to 1937. The *Microtus* and *Peromyscus* data were obtained from captures while those of *Blarina* were obtained primarily from signs.

I wish to thank Dr. W. H. Burt for making available to me the data concerning *Peromyscus.* My wife, Mary Ruth, made many of the compilations of the *Microtus* data.

STUDY AREAS

Data were obtained from three habitats, an abandoned field ("old field"), a grass-sedge marsh, and an oak-hickory wood lot, all located in southeastern Michigan. I have described the first two habitats elsewhere (Getz, 1961b). In brief, the old field supports a sparse stand of *Poa compressa* (65 gr/M^2) with a few scattered forbs (*Daucus Carota, Solidago* spp., and *Potentilla intermedia*). The soil is relatively dry throughout most of the year. The marsh supports a dense stand of grasses and sedges (325 gr/M^2). From October to June the surface is inundated in most places; when not inundated, the substrate is almost completely saturated. In comparison with the old field, the marsh is the more favorable vole habitat (Getz, *op. cit.*). The data pertaining to *Peromyscus* were obtained from an oak-hickory wood lot. For a description of this habitat see Burt (1940).

METHODS

TRAPPING

The entire old field (2.5 hectares) and a 4.4 hectare portion of the marsh were grided with a 12-meter interval. The stations so established were trapped for five days each month September, 1957, through September, 1958. Because of the large number of stations in the marsh, two trapping periods were required to cover all stations. For the first four days of a trapping period the traps were checked twice a day, 0800 to 1100 and 1600 to 1800. On the fifth day the traps were checked only in the morning, at which time they were picked up and moved in preparation for the next trapping period. Wooden multiple-catch traps of the type described by Burt (1940) were employed throughout the study. Bait consisted of equal amounts of sunflower seeds and commercial chicken scratch (cracked

corn, wheat, oats, millet, and buckwheat). No prebaiting as such was employed. Traps were placed at the stations at least one day in advance of a trapping period (upside down, with the doors open). The traps normally contained bait from the previous period, which may have served as prebaiting. Individuals were marked by toe clipping.

The traps utilized were not efficient in holding *Blarina* since most of the shrews were able to open the trap-door and escape. As a result few actual captures were recorded. From the odor and feces in the trap, however, it was possible to determine that a trap had been entered by this species. Much information in the form of signs, therefore, was obtained concerning *Blarina*.

Burt used the same type of trap, positioned in a slightly larger grid (13.5-meter interval). Since he was studying a nocturnal species, his traps were normally checked only in the mornings. The trapping periods were six days long with an interval of one week between periods. Hemp seeds were used as bait. No prebaiting was employed in the study. The individuals were marked by a combination of ear punching and toe clipping.

ENVIRONMENTAL FACTORS

A dial maximum-minimum thermometer (U.S. Weather Bureau type) was placed in the old field and marsh to record temperatures at the level of the vole runways. During the period of June through September a second thermometer was placed in a site in the old field where the vegetation was more sparse than at the permanent station. Readings were made each time the traps were checked.

A record was made each day as to the weather conditions. In the analysis of the data, a day was considered to be cloudy if the sun was covered for more than half of the day. A day was considered to be "rainy" if any rain at all fell. Data concerning rainfall and intensity of moonlight were not recorded during the night. Burt kept general notes as to whether the night had been clear, cloudy, or rainy. He has discussed the influence of weather upon the activity of *P. leucopus* elsewhere (Burt, 1940).

RESULTS

RESPONSE TO TRAPS

Time to capture the known population.—In making comparisons of population densities of a species in different habitats, one must assume that the trapping technique employed is equally effective in all or make allowances for any differences. Since the marsh and old field differed markedly in environmental conditions, the *Microtus* data have been analyzed to determine the relative effectiveness of the trapping technique used in the study in these two areas.

One cannot always be certain that the entire population of an area has been trapped; certain individuals may avoid the traps and

never be captured (Pearson, 1959). Because of this, it is necessary to use the known population (i.e., those individuals known to be present) to determine the rate at which the population was captured in each area. Thus, while a lesser percentage of the population was captured initially in the old field, by the afternoon of the second day approximately the same percentage of the known population was captured in both areas (Fig. 1). There is no significant difference in the rate of capture from the second through the fifth day. Likewise, there is no significant difference between the areas in regard to the individuals known to be present, but not captured a given period (3 and 4% for the marsh and old field, respectively).

Comparison of unmarked and marked individuals.—Microtus: As stated above, the marsh was trapped in two periods each month,

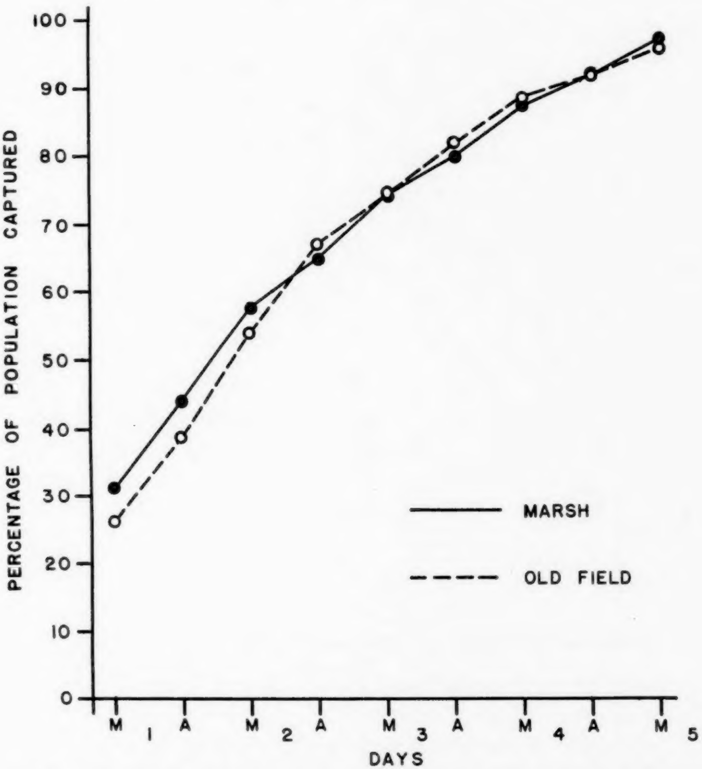

Fig. 1.—Rates of capture (live-trap) of the known population of *Microtus pennsylvanicus* in marsh and old field habitats; based on 13 trapping periods in each habitat. M, morning check of traps; A, afternoon check.

about half of the study area being trapped each period. Those individuals whose home ranges were on the boundary between the two sections were often captured during both periods. Since comparisons of unmarked individuals with those marked the previous month were desired, inclusion of these animals in the analysis of the recaptures would bias the results. To avoid this bias, only data from the first period of each month have been included in the discussion of recaptures in the marsh.

The unmarked individuals appearing on an area represent individuals immigrating or leaving the nest since the last trapping period. Such processes occur continuously and thus are taking place during a trapping period. If one considered all the new individuals caught a given month to have been present the first day of trapping, estimates of the percentage captured each day would be biased (too

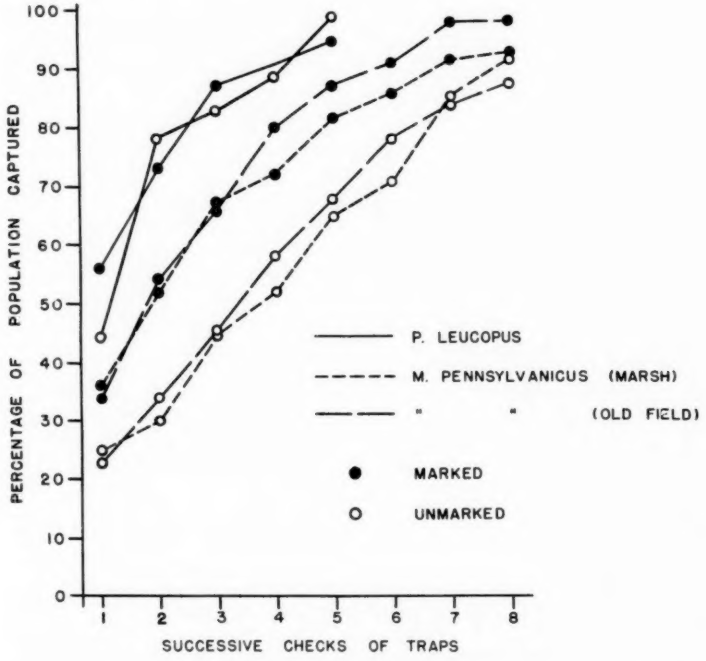

Fig. 2.—Rates of capture of marked and unmarked individuals of *Peromyscus leucopus* and *Microtus pennsylvanicus*. Traps for *P. leucopus* were checked once a day, in the morning; those for *M. pennsylvanicus* twice a day, morning and afternoon. *P. leucopus* data based on 5 trapping periods; *M. pennsylvanicus* data based on 13 trapping periods in each habitat.

low). To avoid this bias, the average number of new individuals appearing on an area each day was computed. In determining the rate of capture of the unmarked individuals, only the number predicted to have appeared by the time of each trap-check has been used in calculating the percentage captured.

Comparisons of rates of capture of the two groups of individuals

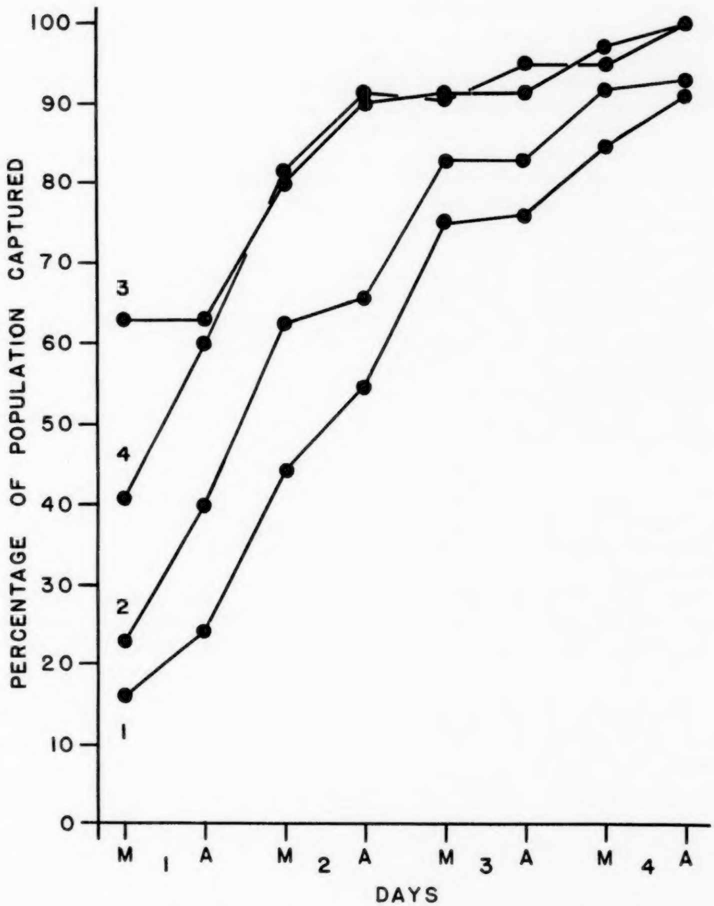

Fig. 3.—Initial rate of capture (1) and rates of capture for subsequent 3 months (2-4) for individuals of *Microtus pennsylvanicus* first captured in June, 1958. The number of individuals included in each sample are 54, 30, 30, and 21 for 1 through 4, respectively.

clearly show that the individuals marked the previous month were captured more readily than were the unmarked animals (Fig. 2). This was true during all months in both areas except for the month of April in the marsh. During this month, the rate of capture of unmarked individuals was slightly greater than that for the marked ones.

It was also desired to determine if the rates of capture became greater during subsequent trapping periods (i.e., with more exposure to traps). To do this, the recapture data for the individuals first captured a given month were studied to see if those individuals that survived were recaptured more readily the more periods they remained on the area. The data for most months indicate that the rate of capture increased up to the third period. Since the average survival time of *M. pennsylvanicus* was less than three months (Getz, 1960), insufficient data were available to determine rates of capture after the third month. Data for the group with the best survival is given in Figure 3.

Peromyscus.—Only five trapping periods were found to have enough unmarked individuals appearing between periods to allow comparisons between the responses of marked and unmarked individuals. These data show that unlike *M. pennsylvanicus,* the individuals captured the previous trapping period were not more readily captured than were the unmarked individuals (Fig. 2). Tanaka (1956), utilizing part of Burt's data in a different manner, also found *P. leucopus* to be isoresponsive.

RESPONSE TO WEATHER CONDITIONS

Microtus.—Hamilton (1937) has shown *M. pennsylvanicus* to be primarily crepuscular and diurnal in habits. During the present study the traps were checked after dawn and just before dusk. The captures recorded in the morning, therefore, represent those individuals that entered the traps during the two peaks of crepuscular activity as well as during the night. Those captures recorded in the after-

TABLE I.—Influence of weather upon the activity of *Microtus pennsylvanicus* (based on 5369 and 1043 captures in the marsh and old field, respectively)

Weather	Percentage of population caught			
	Marsh		Old field	
	Day	Night	Day	Night
Rainy	14		20	
Cloudy	21		20	
Sunny	19		21	
Above 20° C	12	33	10	41
Below 0° C	21	41	8	17
Average (all conditions)	19	36	19	34

noon check of the traps, however, represent individuals active during the day. This facilitates comparison of the captures with daytime weather conditions.

There was no difference in the captures on cloudy days in comparison with sunny days (Table I). This was true in the old field, where the vegetation was sparse, as well as in the marsh which had much more cover. In the marsh there were slightly fewer captures those days during which it rained than on days that no rain fell. No difference was evident in the old field.

The most obvious influence of temperature upon the activity of the voles was observed in the old field. During the summer when the temperature was above 20° C there were fewer captures during the day and more at other times (Table I). Apparently, when daytime temperatures become extremely high, diurnal activity is abandoned in favor of increased nocturnal and/or crepuscular activity.

During the winter when the temperatures dropped below 0° C, captures were fewer in the old field both during the day and night. This was especially true of January and February. During January and February, 62 and 89 per cent, respectively, of the known population was not captured. That these individuals were resident on the area was indicated by the presence of surface nests after a cover of snow had melted. Presumably their activities were restricted to such an extent that they did not range far enough to encounter traps.

Data from the marsh also indicate that the voles are less active on days during which the temperature rises above 20° C. The nocturnal and crepuscular activity under such conditions was also slightly less, however. There was no decrease in the numbers of captures in the marsh on days or nights during which the temperature dropped below 0° C. There were actually slightly more captures during such nights.

The more extreme temperatures in parts of the old field may contribute to the difference in responses in the two areas. The thermometer in the more exposed part of the field (and where the voles were most abundant) indicated especially high daytime temperatures in the summer (7 to 10° C above those in the marsh). Winter temperatures were also probably more extreme (temperatures were obtained only during the months of June through September). Although 20 and 0° C have been used as delimiting temperatures for comparing amounts of activity in both areas, the temperatures

TABLE II.—Influence of weather upon the diurnal activity of *Blarina brevicauda* in a grass-sedge marsh (data compiled from entire study)

Weather	No. signs during day	No. signs previous night	Relative amount diurnal activity
Sunny	168	279	60%
Cloudy	108	101	107%
Rainy	183	263	70%

in the old field were more extreme. A greater modification of the activity pattern, therefore, resulted.

Blarina.—The data concerning *B. brevicauda* involve the use of signs rather than actual captures and cannot be analyzed in the same manner as were the *M. pennsylvanicus* data. Since shrews prefer a cool, moist atmosphere (Pearson, 1959; Pruitt, 1959) nights would normally have more favorable atmospheric conditions than would days, especially during the summer. The relative amount of diurnal activity (number of signs recorded during the afternoon check of the traps divided by the number recorded during the morning check) has been used to determine the influence of sunshine and rain upon the activity of this species.

There were fewer signs in the marsh on sunny days than on those that were cloudy or rainy (Table II). Also there were fewer signs when it rained than when it was merely cloudy. Cloudy days appear particularly favorable as more signs were recorded during such days than the preceding nights. Less activity on sunny days may be a response to lower humidity conditions rather than to sunshine itself; humidity measurements were not obtained in the present study, however. During June through August daytime activity was less under all conditions than at other times of the year (sunny, 37; cloudy, 50; rainy, 67% of the crepuscular and nocturnal activity). The same general conclusions appear to apply to the old field. This area was too dry to support a large population of shrews throughout the year (Getz, 1961c). As a result there were too few data for analysis.

Temperature variations had no marked influence upon the activity of *B. brevicauda* in the marsh. Signs were only slightly fewer (3 to 4% below average) on nights the temperature dropped below 0° C and on days it rose above 20° C. Temperature extremes may have combined with the dryness of the substrate to make the old field an unfavorable shrew habitat. The data were too few to determine the influence of temperature upon the activities of the short-tail shrew in this habitat.

Discussion and Conclusions

All species of small mammals do not respond in a similar manner to live-traps. In some species, the unmarked individuals are less readily captured than are the ones captured previously, in others the reverse is observed, while still others are isoresponsive. To accurately determine population densities from trapping data, one must, first determine the response of individuals of each species to the traps. The data involving those species not isoresponsive must then be corrected to obtain valid estimates of population densities.

Microtus pennsylvanicus was found to be similar to *M. montebelli* (Tanaka, 1956), *M. agrestis* (Chitty and Kempson, 1949), *Peromyscus maniculatus,* and *Clethrionomys gapperi* (Morris, 1955) in that marked individuals were more easily captured, even after an in-

terval of a month, than were the unmarked individuals. Unmarked individuals of *Peromyscus leucopus*, on the other hand, were captured as readily as were the marked ones.

Responses to weather conditions also vary. In the present study *Blarina brevicauda* was found to be less active on sunny days while *M. pennsylvanicus* was just as active on such days as it was on cloudy days. Furthermore, the activity of *M. pennsylvanicus* was influenced by temperature variations. The responses of each species to the weather conditions occurring during a trapping period must, therefore, be determined and compensated for in obtaining estimates of population densities (this would apply particularly to short period snap-trapping).

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Plants of Fargo, North Dakota[1]

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ABSTRACT: A list published in 1921 included 540 species and now 125 more are added. Some of these were overlooked before, many new weeds have been introduced and some cultivated plants have become established. About 20 species that did not occur naturally in the area, but did occur on higher ground a few miles distant, have become established in sand used as ballast for railroad tracks. Probably five or six species have disappeared and a dozen others are endangered by conversion of a wooded area into suburban homes. Other changes in status are noted. Only small remnants of prairie persist.

A list of the wild plants in the vicinity of Fargo, North Dakota and Moorhead, Minnesota was published (Stevens, 1921) which included 540 species. Since that date additional species have been introduced and some native plants have disappeared. The present supplement to that list records some 125 additional species that have been observed over the 40-year period. The names used here are those of Gray's Manual, 8th ed., and no note is made of changes from the previous list except for a few errors. Neither are flowering dates included here. Revised dates for weeds have been published (Stevens, 1956) and a complete list is in preparation.

The area included is approximately 10 miles in diameter. Only the Red River Valley is represented, with the river bank and its narrow fringe of trees, fields, roads and city environs. The soil is silt or clay with no natural sand or stones. Occasional drainage channels furnish a wetter habitat while the ridges of artificial drains and road grades provide drier places. If the area were extended to a 50 mile diameter it would include some of the sandy Sheyenne Delta to the southwest and higher ground beyond the valley to the east thus adding materially to the list of species.

The original prairie flora can be judged only from very small remnants in cemeteries and along roadways where invasion of immigrant species is often heavy. Timbered areas have suffered as much in recent years from pasturing and from urban developments. Increases in park areas have resulted in removal of undergrowth, development of playgrounds, etc. Edgewood Golf Course now occupies the largest river bend which was formerly one of our favorite places. A limited flora still persists on one edge but most if not all of the *Crataegus mollis* and *Populus tremuloides* have been removed. The one colony of *Solidago flexicaulis* persisted nicely until a few years ago.

On the Minnesota side of the river, northward from the above

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[1] Contribution from North Dakota Institute for Regional Studies, Journal Series, Paper No. 11.

area, were many acres of *Populus tremuloides*. Much of this is now occupied by suburban homes and *Viola conspersa, Monotropa uniflora, Pyrola elliptica, Thalesia uniflora, Senecio aureus*, and *Petasites sagittata* are probably gone. Others that have been reduced and may be lost are: *Oryzopsis asperifolia, O. racemosa, Schizachne purpurascens, Uvularia sessilifolia, Smilacina racemosa, Anemone quinquefolia, Rubus pubescens, Desmodium glutinosum* and *Geranium maculatum*.

Recently introduced species are mostly accounted for in the present list. Roadsides have become less productive for collecting because of road widening, surfacing and occupation largely by *Bromus inermis, Melilotus* and *Lactuca scariola*. Chemical control of railroad edges has nearly eliminated one large source of new weeds.

One feature of special interest is the arrival of native species in the gravel ballast for railroads. Many that were not originally present appear occasionally and some have become well established. The recent use of crushed granite for ballast has tended to reduce this list. In 1938 the Northern Pacific Railway raised its tracks several feet for the Thirteenth Street subway. The sand used there shows a nice growth of *Equisetum hiemale, Sporobolus cryptandrus, Cyperus schweinitzii, Petalostemum purpureum* (present in prairie), *Lithospermum incisum* and *Helianthus petiolaris* as well as *Cenchrus longispinus, Stipa comata*, occasional *Astragalus striatus, Artemisia glauca*, the one *Prunus pumila* and other species.

LIST OF SPECIES

Juniperus virginiana L., Eastern Red Cedar.—Along the river near Fargo in 1959, J. R. Nelson. Doubtless a seedling from planted trees.

Typha angustifolia L., Narrow-leaved Cattail.—First noticed in 1958 but must have been here for some years. It seems to be increasing rapidly.

Potamogeton foliosus Raf.—Roadside ditch in 1952.

P. zosteriformis Fern., Flatstem Pondweed.—Collected by L. R. Waldron in 1902.

Triglochin maritima L., Arrowgrass.—Occurs at Moorhead and Dilworth, Minnesota.

Poa annua L., Annual Bluegrass.—First noted in 1920 and has become rather common in moist and bare places in lawns and waste corners.

Glyceria borealis (Nash) Batch., Northern Mannagrass.—There is a specimen labeled Fargo, July 5, 1898. We have not seen it in recent years.

G. striata (Lam.) Hitchc., Fowl Meadowgrass.—Collected north of Moorhead in 1955.

Bromus ciliatus L.—No specimens at hand from Fargo but several from adjacent areas.

B. tectorum L., Downy Bromegrass.—Abundant by railway elevator in Moorhead in 1958.

Puccinellia nuttalliana (Schultes) Hitchc., Alkali Grass.—Occasional in wet, saline soil.

Agropyron cristatum (L.) Gaertn., Crested Wheatgrass.—First collected in 1937 on town lot.

Diplachne fascicularis (Lam.) Beauv.—Found in 1955 around a lumber yard; also in Moorhead in 1958.

Calamovilfa longifolia (Hook.) Scribn., Big Sandgrass.—Along railroad in 1923.

Buchloe dactyloides (Nutt.) Engelm., Buffalograss.—A small spot in native prairie, found in 1921, was soon destroyed by industrial developments.

Muhlenbergia asperifolia (Nees & Mey.) Parodi, Scratchgrass.—Low prairie by railroad.

M. richardsonis (Trin.) Rydb. Previously cited as *M. cuspidata* which does not occur in the area.

Setaria verticillata (L.), Bur Pigeongrass.—First noted in 1922, it has become frequent and quite a nuisance around gardens and neglected town lots.

Digitaria sanguinalis (L.) Scop., Common Crabgrass.—This has been found several times in recent years and gives some evidence of persisting.

Panicum perlongum Nash.—Has not been collected again and probably was destroyed at the original station.

P. wilcoxianum Vasey.—On railroad ballast in 1942.

Andropogon scoparius Michx., Little Bluestem.—Frequent.

Carex sprengellii Torr., Long-beaked Sedge.—Collected at Fargo in 1921, now perhaps destroyed.

Carex atherodes Spreng., Slough Sedge.—Frequent in wet places.

C. cristatella Britton, Crested Sedge.—Along river bank in 1933.

C. tetanica Schk., Wood's Sedge.—Collected in 1920.

C. torreyi Tuckerm., Torrey's Sedge.—Woods north of Moorhead in 1959.

C. saximontana Mack., Rocky Mountain Sedge.—Same as last, frequent.

Lemna perpusilla Torr., Minute Duckweed.—Collected by L. R. Waldron in 1908.

Cyperus acuminatus Torr. & Hook.—Frequent in low places.

C. schweinitzii Torr.—In sand ballast on railroad since 1942.

Eleocharis calva Torr.—Frequent in wet places.

Ulmus pumila L., Siberian Elm.—Natural seedling collected in 1954.

Parietaria pensylvanica Muhl., Pellitory.—Not collected until 1926 but presumably overlooked as it proves to be quite common here and elsewhere.

Juncus gerardi Loisel., Blackgrass.—Found in railroad ditch in 1954.

Zygadenus elegans Pursh, Camas.—A specimen by Lee in 1891 is labeled Fargo but I have not seen it in the present area.

Commandra pallida A.DC., Bastard Toadflax.—Perhaps overlooked before. It was collected in 1936 on railroad ballast and may have occurred in native prairie.

Polygonum amphibium L.—I find no confirmation of this but the variety *stipulaceum* (Coleman) Fern. is growing on railroad sand ballast. I have not found it in flower but it usually is cut down prior to blooming.

P. hydropiper L. Waterpepper.—Collected in 1939 and at Wild Rice (10 mi. south of Fargo) in 1924.

P. prolificum (Small) Robins.—This has been called *P. exsertum*. It is a slender plant that grows among grasses or on bare soil in low areas.

Rumex domesticus Hartm., House Dock.—Not recognized until 1955 when it was fairly common. The specimen previously reported as *R. occidentalis* is now placed here.

R. stenophyllus Ledeb.—First noted in 1955; frequent.

Chenopodium berlandieri Moq., Pit-seed Goosefoot.—This grows in broken places in grassland or along road and dry ditches, not so often in fields.

C. strictum Roth, Late Lambs Quarters.—This was not noted until about 1930 but one specimen identified by Wahl (1954) was collected in 1917. It has become very common, especially as a street and yard weed, also in fields since about 1945. Its flowering period (late August) is characteristic.

C. album, var. *stevensii* Aellen.—This variety was based on Fargo material. It seems rare but perhaps is common according to Wahl's interpretation.

C. bushianum Aellen., Bush's Goosefoot.—Frequent in wooded areas. Previously not distinguished from *C. album.* The forma *acutidentatum* (Aellen, 1929: 119) was based partly upon Fargo material.

Atriplex patula L.—The slender, typical form has become very aggressive in yards and gardens since 1921.

A. rosea L., Redscale.—This was found around streets in 1923 and invaded lawns to some extent, but seems to have disappeared.

A. glabriuscula Edmonston.—Well developed colonies of this were found in 1954 and 1955.

Cycloloma atriplicifolium (Spreng.) Coult., Tumbleweed.—Found in some abundance in the railroad yards at Dilworth, Minnesota, in 1958.

Kochia scoparia L., Burning Bush.—Has become exceedingly abundant and aggressive.

Salsola collina Pallas.—This seems the common form now. Determined by Aellen.

Amaranthus hybridus L.—A single plant was collected in 1921.

Mollugo verticillata L., Carpet Weed.—This persisted for a number of years about 1920-40, then apparently disappeared from the original location but was seen at another locality in 1953 and found at Jamestown, N.D., also along the railroad.

Agrostemma githago L., Corn Cockle.—Not seen in recent years.

Silene cserei Baum., Smooth Catchfly.—First collected in 1928 and is frequent in gravel ballast along railroads.

Cerastium vulgatum L., Mouse-ear Chickweed.—Appeared in many lawns about 1953 but seems not to persist.

Lychnis alba Mill., White Cockle.—Collected along railroad in 1922 but not found since.

Stellaria longipes Goldie.—The specimen by Bolley is now referred to *S. longifolia* Muhl.

Myosurus minimus L. Mousetail.—Collected at Fargo in 1930 but not seen since.

Alliaria officinalis Andrz., Garlic Mustard.—On a vegetable farm near Moorhead in 1958, well established in edge of woods.

Cardaria draba (L.) Desv., Perennial Peppergrass.—Collected at Moorhead in 1921. Found at Fargo about 1930 and at several places in the county thereafter. The variety *repens* (Schrenk) Schultz appeared in the experiment station plots about 1935 but was eradicated.

C. pubescens (Meyer) Rollins.—This species was found in a bromegrass plot in 1940 where it had been established for some time and still is present.

Lepidium ramosissimum A. Nels., Branched Peppergrass.—One or two plants have been found along streets and railroads. It has not persisted, although it is frequent in similar locations through central North Dakota.

L. perfoliatum L.—One plant was found in 1932 and several at Moorhead in 1958.

Brassica nigra (L.) Koch, Black Mustard.—Found in some quantity in 1955. Previously collected in 1901.

B. hirta Moench., White Mustard.—Found around a seed cleaning plant in 1942.

Camelina microcarpa Andrz., Small-seeded False Flax.—Along railroad in 1955.

Arabis holboellii Hornem.—One plant was found along the railroad in 1947.

Berteroa incana (L.) DC., Hoary Cress.—Along railroad in 1946 and later.

Rorippa sylvestris (L.) Bess.—Collected in 1922 but station since destroyed.

Draba reptans (Lam.) Fern.—Several plants along railroad in 1947.

Sisymbrium officinale (L.) Scop., Hedge Mustard.—There is a specimen collected in 1902. Abundant in a sodded lawn in 1956 but not present the next year.

S. loeselii L.—A few plants were seen in 1956, a number in 1937 at Mapleton, 10 miles west and at Moorhead in 1948.

Descurainia sophia (L.) Webb., Flixweed.—This has become very abundant since 1920.

Hesperis matronalis L., Sweet Rocket.—A frequent escape from gardens.

Fragaria vesca, var. *americana* Porter.—Formerly frequent in aspen woods.

Potentilla anserina L., Silverweed.—A specimen was collected from a city lot in 1953. It was probably introduced there and was soon destroyed. The plant occurs in the Moorhead-Dilworth area but is not common.

Chamaerhodos nuttallii Pickering., Little Rose.—A colony along the railroad in 1947.

Prunus pumila L., Sand Cherry.—A plant brought in railroad ballast about 1940 is still thriving.

Astragalus striatus Nutt.—On ballast of railroad in 1942.

Oxytropis lambertii Pursh., Purple Loco.—On railroad in 1922.

Trifolium resupinatum L.—In lawn in 1941.

T. dubium Sibth.—Collected in new lawn in 1941.

Vicia americana, var. *angustifolia* Nees., Prairie Vetch.—Occasional along railroad.

Geranium pusillum L., Small Cranesbill.—In lawn in 1912.

Euphorbia marginata Pursh., Snow-on-the-mountain.—Frequently escapes from gardens but does not persist.

E. supina Raf. (*E. maculata* L.), Spotted Spurge.—Continues to grow along the railroad and was abundant at Dilworth in 1958.

E. maculata L. (*E. nutans* Lag.), Nodding Spurge.—One plant along railroad in 1929.

Polygala verticillata L., Whorled Milkwort.—Collected near Dilworth, Minn.

Impatiens capensis Meerb. (*I. biflora* Walt.), Spotted Touch-me-not.—This is the common form though *I. pallida* Nutt. has been found occasionally.

Rhamnus cathartica L., Common Buckthorn.—This has become widely established since about 1930.

Althaea officinalis L., Hollyhock.—Continues to volunteer freely.

Malva parviflora L., Small-flowered Mallow.—Common in a garden in 1958.

Elaeagnus angustifolia L., Russian Olive.—First noted as spread from plantings about 1950 and frequently thereafter.

Ammannia coccinea Rottb.—First noted at Fargo in 1923 and at nearby places later.

Epilobium angustifolium L., Fireweed.—Noted about 1920 in a wet spot along the railroad. The plant is only occasional and local in most of North Dakota.

Oenothera serrulata Nutt., Toothed-leaved Evening Primrose.—Collected in 1925. Its continued occurrence is dubious.

Lomatium orientale C. & R., Wild Parsley.—Collected along railroad in 1931.

Anethum graveolens L., Dill.—Commonly persists in gardens.

Cornus stolonifera Michx., Red Osier.—No specimen from the area is at hand but several from nearby.

Lysimachia thrysifolia L., Tufted Loosestrife.—Collected in low ground east of Moorhead.

Apocynum medium Greene.—Material collected in 1951 seems to be this form. It had not been recognized before.

Asclepias speciosa Torr., Showy Milkweed.—Frequent in low, saline soil.

Cuscuta megalocarpa Rydb., Large-fruited Dodder.—Material collected in 1950 seems referable to this form.

Amsinckia retrorsa Sucks., Buckthorn weed.—Collected along railroad in 1942 but soon destroyed.

Hackelia virginiana (L.) I. M. Johnston.—This was recognized in 1953 as abundant in one river bend and a specimen collected in 1934 is this species. It seemed not affected by a leaf spot which was abundant on *H. americana.*

Verbena rigida Spreng.—Plants were growing among trees on the Agricultural College campus in 1943 but did not persist.

Glechoma hederacea L., Ground Ivy.—Collected in Moorhead in 1921 and in Fargo in 1955.

Galeopsis tetrahit L., Hemp Nettle.—Along railroad in Moorhead in 1960.

Molucella laevis L., Shellflower.—Collected in Moorhead in 1959 where a house may have been removed (flood-control project).

Hedeoma hispida Pursh., Rough Pennyroyal.—Along railroad in 1925; in newly sodded lawn in 1959, few the next year.

Salvia reflexa Hornem., Lance-leaved Sage.—Collected in 1933 on roadside and in 1958 on river bank near Moorhead.

Solanum dulcamara L., Bittersweet.—In dooryard at Fargo, not known to have been planted.

Physalis heterophylla Nees.—Along railroad, 1921 and later.

Penstemon albidus Nutt., White Beardtongue.—Along railroad in 1925.

Plantago eriopoda Torr., Alkali Plantain.—Collected at Moorhead in 1921.

P. indica L.—Along railroad at Dilworth in 1958.

Galium trifidum L., Small Bedstraw.—Collected north of Moorhead in 1955.

Lonicera tatarica L., Tartarian Honeysuckle.—Volunteers freely from plantings.

Sambucus canadensis L., Black-berried Elder.—Collected in Moorhead in 1959, probably escaped from plantings.

Campanula rapunculoides L., Creeping Bellflower.—This is often planted and has spread into lawns in recent years.

C. rotundifolia L., Blue Bell.—Along railroad in 1925.

Liatris punctata Hook., Narrow-leaved Blazing Star.—Along railroad in 1920.

L. pycnostachya Michx., Tall Blazing Star.—This occurs in low prairie along the railroad at Dilworth.

Chrysopsis villosa Pursh., Golden Aster.—Frequent along railroad since 1917.

Solidago flexicaulis L., Broad-leaved Goldenrod.—This still grows where it was found in 1915, the area now in the Edgewood Golf Course.

Aster sericeus Vent., Silky Aster.—Along railroad in 1920; common at Muskoda, 15 miles east.

Antennaria microphylla Rydb.—A specimen labeled "Fargo, Field in 1891" has been verified by Cronquist but the plant has not been seen recently.

Helianthus nuttallii T. & G., Nuttall's Sunflower.—A Fargo specimen was determined as this by E. E. Watson.

Coreopsis tinctoria L., Tickseed.—Some plants persisted for many years along the edge of a field near Fargo.

Bellis perennis L., English Daisy.—A few plants in flower were found in a lawn in 1955.

Echinacea angustifolia DC, Purple Coneflower.—Along railroad in 1923.

Galinsoga ciliata (Raf). Blake., Quickweed.—This has appeared in several places since 1937 and seems now established.

G. parviflora Cav.—Found in flowerpot in 1929 and in door yards in both Fargo and Moorhead in 1958.

Matricaria maritima L., Scentless Chamomile.—Two plants by railroad in 1958.

Arctium tomentosum Mill.—A colony, apparently two or three years old, was found in 1956.

Carduus acanthoides L., Welted Thistle.—One plant was found in 1940, a large colony at another place in 1947 and some at another location in 1956.

Artemisia glauca Pall., Green Sage.—Along railroad in 1942 and later.

Centaurea repens L., Russian Knapweed.—A colony in a bromegrass pasture on the college grounds was first noticed in 1937.

C. maculosa Lam., Spotted Knapweed.—A few plants were found along the railroad in 1956 but were destroyed the next year. It had been established in a farmyard about 20 miles east for many years.

Lygodesmia juncea (Pursh) D. Don., Skeleton Weed.—Along railroad in 1934.

Tragopogon major Jacq., Goatsbeard.—This is the only form found here.

Taraxacum koksagyz Robin., Russian Dandelion.—A few plants where seed had been cleaned in 1942 but none had been found near the field where plants were grown. They are well established near our building; begin flowering at the same time as *T. officinale,* but flower heads remain open until late afternoon.

Crepis tectorum L., Hawk's-beard.—Along railroad in Moorhead in 1958.

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Some Ecological Characteristics of the Molluscan Fauna of a Typical Grassland Situation in East Central Kansas[1]

PAUL F. BASCH, PHILIP BAINER and JERRY WILHM[2]

ABSTRACT: A survey of some of the ecological associations of the molluscan fauna found in a typical grassland situation was conducted on the Ross Natural History Reservation, Lyon and Chase counties, Kansas, during the summer of 1960. The collecting stations were selected for their differences in habitat conditions, and soil or water analyses were conducted at each. Associated vegetation was studied in detail.

Six species of aquatic mollusks and 16 species of terrestrial snails were collected. *Physa hawnii* was the most common aquatic snail found, and *Gastrocopta armifera* the most abundant terrestrial species. Two pelecypods, *Uniomerus tetralasmus* and one *Sphaerium*, were found. Many specimens of *Pupoides albilabris*, *Gastrocopta procera*, *Zonitoides arboreus*, *Vallonia parvula*, and *Succinea* sp. were collected. Less abundant species, usually found in moist environments included *Gastrocopta contracta*, *G. tappaniana*, *Helicodiscus parallelus*, *Retinella indentata*, *Hawaiia minuscula*, and *Stenotrema leai aliciae*.

INTRODUCTION

The object of this report is to record some of the ecological associations of the molluscan fauna found in a typical grassland situation. The study area included several different habitats on the Ross Natural History Reservation of Kansas State Teachers College, Emporia.

The reservation is located on the eastern edge of the Flint Hills Upland of east central Kansas. This area of rolling prairie hills crosses the state of Kansas and extends into Nebraska to the north, and southwards into Oklahoma. The hills serve as a sort of ecological barrier, and many species do not extend further west into the drier portions of the state. Since the reservation is in an area that was once cultivated and covered with orchards, and is still grazed, the information included in this study should be useful in determining the changes in molluscan populations as the reservation reverts to a natural condition.

HISTORICAL REVIEW OF STUDIES ON KANSAS MOLLUSKS

The Mollusca of Kansas received little attention until the early 1940's, although the earliest studies began over 75 years ago. In 1884, F. W. Cragin began a series of surveys of the flora and fauna of the state, sponsored by Washburn College in Topeka. Cragin was

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also editor of the *Bulletin of Washburn Laboratory of Natural History.* In this bulletin, R. Ellsworth Call published a series of papers on the molluscan fauna of Kansas, and Binney and Gray (1885) listed land shells of northeast Kansas.

Hanna (1909) mentioned 75 species and subspecies of gastropods in Douglas County and in the drift along the Kansas River. Franzen and Leonard (1942) conducted a preliminary survey of Kingman County, Kansas, and collected 26 species and subspecies of gastropods. Franzen and Leonard (1943) reported 16 freshwater mussels and 31 species and subspecies of gastropods from a series of 11 collecting stations in the Wakarusa River valley, a small tributary of the Kansas River. The same year, Alice E. Leonard (1943) reported five species of pelecypods and 21 species and subspecies of gastropods from Meade and Clark Counties, Kansas, most of them from the ungrazed spring areas in Meade County State Park. Franzen (1944) discussed 12 new species and subspecies of gastropods from the eastern two tiers of counties in Kansas. Leonard and Leonard (1946) reported 16 species of unionid mussels, 6 species of aquatic gastropods, and 19 species and subspecies of gastropods from eight collecting stations in Greenwood County, southwestern Kansas. The following year, Franzen (1947) listed the living and fossil Pupillidae of the Sanborn area in northwest Kansas. Franzen and Leonard (1947) reviewed 33 species of living and fossil Pupillidae known in Kansas.

Leonard and Goble (1952) collected 4 species of aquatic mollusca and 21 species of terrestrial gastropods at ten stations selected for their differences in local habitat conditions at the University of Kansas Natural History Reservation. Fitch and Lokke (1956) studied past conditions on the University of Kansas Natural History Reservation as indicated by the durable molluscan shells which persist in the soil long after plant associations and physical features of the environment have changed. Miles (1958) reviewed the three genera and seven species of succineids in Kansas as identified by their soft parts, especially their genitalia, since the shells of some of the succineids are of little taxonomic use. One of the most complete publications on mollusca of Kansas is the Handbook of Gastropods in Kansas by Leonard (1959).

HISTORY AND DESCRIPTION OF THE AREA

The 1040-acre Ross Natural History Reservation is located approximately 4 miles west of Americus or 14 miles northwest of Emporia. The reservation, as described by Hartman (1960), is primarily undulating to rolling bluestem grass prairie. The upland terrain is broken by several shallow ridges and limestone outcrops. A small seasonal creek and several other drainages cross the area. The total Lyon County area is 960 acres and includes portions of sections 7, 8, and 18 in T18S, R9E, section 12 (Hartman, 1960). The remainder of the reservation is in Chase County.

The reservation is located on the east of the Flint Hills Upland and lies in an area once known as Fruitland because of the extensive orchards planted by settlers in the late 1880's. Heavy droughts and recurrent invasions of grasshoppers and chinch bugs discouraged farming and the area is returning to grassland. None of the reservation is under cultivation at the present time. Hartman (1960) records the soils on the reservation as being medium to dark grayish-brown, stony, silty clay loams. Their geologic parent materials are limestone, cherty limestone, calcareous shales, and loess, with most of the soils adapted to native pastures.

The reservation is grazed at present and Hartman reports that there are probably no prairie areas on the reservation that have not been grazed in the last 10 years, although the extent of grazing has varied considerably. The dominant flora of the unbroken upland prairie is little bluestem (*Andropogon scoparius*) and Indian grass (*Sorghastrum nutans*), while the scattered, moderately grazed areas have a thinner cover of little bluestem, side-oats grama (*Bouteloua curtipendula*) and tall dropseed (*Sporobolus asper*).

The major wooded habitats on the reservation include a ravine beginning in Chase County and extending across the county line. A somewhat smaller wooded area lies along the ravine in section A on the eastern edge of the reservation. Several hedgerows are located on the reservation, the most extensive being found along the abandoned roadway of A58, as shown on Figure 1.

The major aquatic habitats include three ponds, the largest of which is Gladfelter Pond in B48. Smaller ponds are located in A5

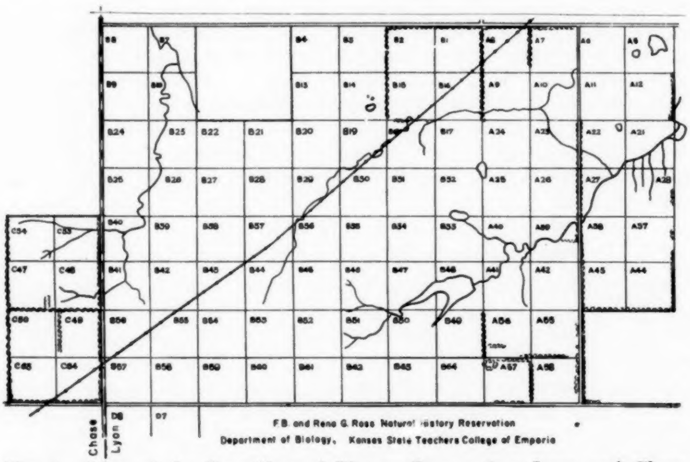

Fig. 1.—Map of the Ross Natural History Reservation, Lyon and Chase counties, Kansas. Each numbered square represents an area of ten acres.

and D10. The reservation is drained by three small streams. One of the streams originates in the wooded ravine in Chase County and flows east, then north. The second forms on the east slope of the upland prairie and flows northeast. The third consists of the watershed for Gladfelter Pond and flows northeast along a winding and wooded course.

Other habitats include several abandoned homesteads, an abandoned limestone quarry in B26, a small spring in A39 and several rocky prairie slopes and prairie washes.

Since acquiring the reservation in 1958, the Biology Department has planted a one-acre feed patch for wildlife in A56, a windbreak and several small groups of evergreens around the headquarters area in A56 and around Gladfelter Pond in B48. Several natural enclosures and lean-to shelters have been constructed and multiflora roses have been planted in different areas to provide protection for wildlife.

CLIMATE

The mean annual rainfall of the county is 34.10 inches; the monthly precipitation varies from an average of 0.81 inches in January to 5.20 inches in May. About 70 per cent of the annual precipitation is received between April 1 and September 30 and the monthly average for this period is 4.04 inches. The total amount of rainfall during the driest year (1936) was 18.13 inches and for the wettest year (1941) 53.37 inches.

The mean annual temperature for the year is 55.8°F, with the monthly average varying from 30.7°F in January to 79.5°F in July. The average temperature from April 1 to September 30 is 68.8°F. The average date of the last killing frost is April 1 and for the first killing frost, October 18. The growing season averages 187 days.

The average relative humidity in Kansas is lower than in states of the east and southeast. The low relative humidity favors rapid evaporation. In the eastern third of the state relative humidity is higher than the rest of the state and ranges from 45 to 50 per cent at mid-day in July to 70 per cent in winter at the same time of day. Most of the year, the prevailing winds are from the south resulting in a drying effect on the soil of the south facing slopes. Most of the above climatological data were abstracted from Flora (1948).

METHODS

Field methods.—A general survey of the reservation was conducted the second week in June, 1960, to select the collecting stations. Following this, collection trips were made on alternate days from June 15 to August 4, 1960. A field sheet kept for each station included a list of dominant flora, a general area description, and a field number for future reference. Shells were placed in small vials for transport to the laboratory. Jewelers' forceps were useful for collecting smaller species. A set of soil sieves was used for recovering specimens from loose soil, gravel, and debris.

Laboratory methods.—The snails were killed and the shells cleaned by immersing them in boiling, soapy water. Removal of the soft bodies of larger specimens proved advisable before they were examined under a binocular microscope.

References used for identification included Pilsbry (1939, 1940, 1946, and 1948), Baker (1928, 1939) and Leonard (1959). Questionable determinations were verified by Mr. Tong-Yun Ho and Mr. Harold Murray of the University of Kansas. The identified specimens were assigned a catalogue number in the mollusk collection of the Kansas State Teachers College, Emporia.

Water analysis.—Water samples were taken at each aquatic station and were checked for dissolved oxygen, carbon dioxide, phenolphthalein and methyl orange alkalinity, total hardness, seston, turbidity, and pH. The test for dissolved oxygen by the Winkler method and tests for carbon dioxide, phenolphthalein and methyl orange alkalinity, and total hardness by the soap method are described by Theroux, Eldridge and Mallman (1943). Seston determination is described by Chandler (1942), and the determination of turbidity with a U.S. Geological Survey turbidimeter, by Welch (1948). The pH was determined with a Beckman zeromatic pH meter.

Soil analysis.—A soil sample was taken at each terrestrial station and was transported to the laboratory in small jars. The sample was then air dried and sifted through a U.S. standard soil sieve with 1.19 mm mesh. Samples were tested for available phosphorus, potassium, and nitrogen, organic matter and pH. All tests were made using LaMotte soil analysis kits as described in the LaMotte Soil Handbook (1956).

COLLECTION AREAS

AQUATIC HABITATS

Three ponds and one stream were surveyed on the reservation. The stream, studied June 23, passes from Gladfelter Pond in B48 and proceeds northeast until it leaves the reservation in A21 (Fig. 1). It is joined by several other small streams in A40, A39 and A27. About one-half of the length is shaded or partially shaded and part is bordered by tall grasses. Except for periods following rains, the width varies from about one to five feet, the depth ranges from several inches to several feet and for the most part the bank is abrupt and bare. Much of the creek bed is over a limestone outcrop and there are many limestone rocks on the creek bottom. Most of the specimens were collected on and under rocks, on vegetation, and on submerged branches. The hardness and methyl orange alkalinity were comparatively high (Table I). Living snails were represented by the largest colony of *Physa hawnii* on the reservation and a few *Lymnaea bulimoides techella* (Table III). Nine *Succinea* sp. were collected at this station and several terrestrial shells were sifted from the bottom mud. *Physa hawnii* was also common in the stream surveyed on the University of Kansas Reservation (Leonard and Goble, 1952).

Three ponds were surveyed on the reservation on July 22. Glad-

felter Pond, located in B48 (Fig. 1), was constructed in June, 1958, and is used by cattle. Almost all of the moluscan specimens were taken from a neck in the southwest corner of the pond. The water was receding and many dead shells were picked up on the drying ground around the edge in this neck. Many living snails as well as a few shells of terrestrial forms were sifted from the bottom silt. *Physa hawnii* was abundant and only 16 *Lymnaea bulimoides techella* were collected (Table III). *Succinea* sp. was fairly abundant at this station.

Two unshaded, mud-bottom pools were surveyed in A5; the larger was about 60 feet in diameter and the smaller about half that, although both were gradually receding. Both ponds serve as a source of water for cattle and were turbid. Limestone rocks were fairly abundant around the edge in the smaller pond and less numerous in the other. The smaller body of water represented the most alkaline condition on the reservation (pH 8.7), the highest temperature (98°F), the highest oxygen content (12.0 ppm), the lowest methyl orange alkalinity (128 ppm), the highest phenolphthalein alkalinity (4 ppm), the softest water (108 ppm), and the lowest per cent of organic material (24.4%) in the seston. The analysis revealed no free carbon dioxide (Table I). Similar results were obtained from the water analysis of the larger pond. *Physa hawnii* was the most abundant snail at this station (Table III). In the smaller body of water *Helisoma trivolvis* and *Sphaerium* sp. were fairly abundant. At the larger pond, two *Bulimulus dealbatus* were found on the dam and several shells of *Uniomerus tetralasmus* were found at the edge. Thus, this station yielded four species not collected elsewhere on the reservation. Leonard and Goble (1952) found *Helisoma trivolvis, Physa hawnii, Sphaerium* sp. and *Succinea concordiales* in a silted pond at the Kansas University Natural History Reservation.

TABLE I.—Water data at the five aquatic stations on the reservation

	Spring A39	Pond B48	L. Pond A5	S. Pond A5	Stream B48-A21
Water Temperature (°F)	59	83	97	98	81
pH	7.2	8.2	8.4	8.7	8.2
Dissolved Oxygen (ppm)	5.8	4.6	5.6	12.0	6.8
Free Carbon Dioxide (ppm)	19.0	0.2	0.0	0.0	2.0
Phenolphthalein alkalinity (ppm)	0.0	0.0	2.0	4.0	0.0
Methyl orange alkalinity (ppm)	315.	165.	135.	128.	265.
Hardness (ppm)	216.	132.	112.	108.	192.
Organic Matter (%)	36.4	27.0	30.7	24.4	27.1
Turbidity (ppm)	....	60.	250.	150.	....

SPRING AREA

The spring area, located in the southeast corner of A39, was surveyed on June 15. This habitat consists of an unshaded body of water about 3 feet wide, 10 feet long, and several inches deep, matted with watercress *(Nasturtium officinale)* and bordered at the head and on the sides with limestone rocks. The water seeps down a gradual northeast-facing slope forming a marshy environment with an abundance of great bulrush *(Scirpus validus)*. Clumps of Indian grass and big bluestem *(Andropogon gerardi)* surround the limestone rocks.

An analysis of the spring water revealed that the water contained the highest free carbon dioxide content (19.0 ppm), the highest methyl orange alkalinity (315 ppm), the greatest hardness (216 ppm), the lowest pH (7.2), and the lowest temperature (59°F) (Table I). The results obtained from the water analysis at this station were in direct contrast to those obtained from the small pond in A5. In the soil surrounding the spring the pH and the nitrogen content were higher than at any other area surveyed (Table II). Organic matter was comparatively high. Burch (1955) found a close correlation between organic matter and the distribution of snails.

Twelve species of mollusks were taken from the spring area (Table III), mostly from the moist soil under the limestone rocks. The three most abundant species were in order: *Gastrocopta armifera, Succinea* sp., and *Vallonia parvula,* and these comprised about 70 per cent of the collection. Over 16 per cent of the specimens were *Pupoides albilabris* and *Retinella indentata.* Thus, the remaining seven species

TABLE II.—Soil data from the 16 terrestrial stations on the reservation

Station	pH	N (lbs/-acre)	P (lbs/-acre)	K (lbs/-acre)	Organic (%)
Spring (A39)	7.6	32	200+	120	5.18
Decaying log (C33)	7.4	8	150	185	3.01
Wooded area (A21)	7.4	8	200+	155	4.72
Wooded area (C33)	7.4	24	150	110	1.92
Hedgerow (A42-A39)	7.2	3	200+	140	5.31
Hedgerow (B1-B16)	7.4	8	200+	275	3.45
Abandoned farmsite (C63)	6.8	8	200+	275	4.92
Prairie wash (B4)	7.4	3	200+	90	2.98
Limestone quarry (B39)	7.4	3	200+	135	2.09
South facing slope (D7)	7.4	8	200+	160	6.03
West facing slope (B26)	6.0	8	200+	125	5.38
Limestone ledge (C33)	7.4	3	200+	90	6.62
Prairie area (A6)	6.0	3	150	140	4.49
Prairie area (B35)	6.2	24	200+	160	4.69
Prairie area (B53)	6.6	3	200+	150	4.72
Prairie area (B8)	6.2	3	150	120	3.90

comprised only 14 per cent of the collection. Ten of the 11 *Lymnaea parva* taken during the study were collected at this habitat and this was one of two stations in which *Gastrocopta tappaniana* was collected. This was the most prolific station for *Hawaiia minuscula*. The nearby area produced a few *Succinea* sp. and no snails were found among the matted watercress roots.

DECAYING LOG

A decaying log located in the heavily wooded area of C33 was studied on July 15. The log was about one foot in diameter and two and one-half feet long, and was easily broken into small pieces for study. The soil underneath the log was rich and moist. Only three species were collected at this station and only *Zonitoides arboreus* was found in abundance. This species was also abundant in a decaying log surveyed on the Kansas University Natural History Reservation (Leonard and Goble, 1952).

WOODED AREAS

Two wooded areas were surveyed on the reservation. The wooded habitat along the stream in the south part of A21 was surveyed on June 17. On the gentle slopes, clumps and scattered trees of cottonwood *(Populus deltoides)*, box elder *(Acer negundo)*, green ash *(Fraxinus pennsylvanica)*, osage orange *(Maclura pomifera)*, and black walnut *(Juglans nigra)* occur in the area. Several thickets of fragrant sumac *(Rhus aromatica)* and dogwood *(Cornus drumindii)* were noted near the creek. The floor of this wooded area is shaded and moist. Rotting logs and moist humus on loose rich soil served as profitable collecting areas.

On July 28, a survey was made on the most heavily wooded area on the reservation, in C33. The largest trees in this area are hackberry *(Celtis occidentalis)*, American elm *(Ulmus americana)*, red elm *(Ulmus rubra)*, black walnut and osage orange. Thickets of fragrant sumac, coralberry *(Symphoricarpos orbiculatus)*, and dogwood are found on the slopes. Also patches of gooseberry *(Ribes missouriense)*, gaura *(Gaura parviflora)*, poison ivy *(Rhus radicans)* and ironweed *(Vernonia baldwini)* inhabit the floor of this area. Some of these plants came in from the nearby prairie area. The undercover is heavily trampled by cattle. There are a few small limestone rocks and many large logs and brush piles which served as excellent collection sites. No unusual soil conditions were noted at either of the wooded habitats, except that the organic matter in C33 was low (Table II).

Thirteen species were collected in A21 and only eight in C33 (Table III). However, the latter collection was made during drier conditions. The A21 wooded area yielded more species than any other collecting station. *Gastrocopta armifera* was the dominant mollusk of both wooded areas, comprising about 40 per cent of the collection in each. *Vallonia parvula* and *Zonitoides arboreus* comprised over 36 per cent of the A21 collection. Thus, the remaining ten species com-

prised only 23 per cent of the collection. The A21 area was the most profitable area on the reservation for *Gastrocopta contracta* and this station was one of two in which *Gastrocopta tappaniana* was collected. Seven species were represented in the A21 wooded area which were absent in the other habitats. However, *Stenotrema leai aliciae* was collected only in C33. About two-thirds of the collection in C33 represented *Gastrocopta armifera* and *Zonitoides arboreus*. *Vallonia parvula,* very common in A21, was not as abundant in C33 and *Succinea* sp. was twice as abundant in C33.

HEDGEROWS

Two hedgerows were surveyed on the reservation. One, located on the east border of A39 and A42, was surveyed July 20. The dominant tree is osage orange and interspersed are honey locust *(Gleditsia triacanthos),* American elm, and hackberry with some thickets of dogwood and sumac nearby. The ground slopes and is heavily shaded and contains loose, wet soil, sparse vegetation, a few limestone rocks, and has abundant leaf litter and twigs. The hedge contains a high percentage of organic matter in the soil compared to the other areas (Table II).

The second hedge, located on the east border of B1 and B16, was studied August 2, and contains osage orange with scattered honey locust and American elm. Most species were collected in the heavy litter and leaves on the loose, moist soil. Very little ground vegetation exists. The potassium content was relatively high at this station (Table II). Burch (1955) stated that potassium may have some indirect effect, but is not assumed to be a limiting factor.

Ten species were taken from the A42-A39 hedgerow, which was the richer of the two hedges in terms of species and individuals (Table III). *Gastrocopta armifera* comprised over 34 per cent of the collection and *Vallonia parvula* over 24 per cent. *Retinella indentata, Zonitoides arboreus* and *Stenotrema leai aliciae* were fairly abundant at A42-39, but were not taken from the other hedgerow. Although seven species were collected at the B1-16 hedgerow, only *Vallonia parvula* and *Gastrocopta armifera* were abundant making up 88 per cent of the collection. *Succinea* sp. was fairly abundant at the B1-16 hedge and only one was collected at the other hedge. The more prolific hedge also contained the only *Gastrocopta pentodon* collected on the reservation.

ABANDONED HOMESTEAD

One abandoned homestead in C63 was surveyed on August 4. The limestone shell of a farmhouse still stands and many limestone rocks are located around the house. Because of the artificial situation, there is a wide variety of plants in the area. Apparently, winter and spring precipitation accumulates in the dirt cellar. A high potassium content was measured in the soil sample taken from the cellar floor (Table II). Nineteen shells of *Physa hawnii* were collected on the

moist floor (Table III). Nine *Gastrocopta armifera* were found around the farmhouse.

LIMESTONE OUTCROPS

Five limestone outcrops were surveyed. Van Cleave (1953) states that mollusks are intimately dependent upon a lime supply for the production of their shells and the correlation is so close that collectors of shells have long realized that limestone outcrops and streams flowing through limestone are favorable collecting areas. Burch (1955) reports that calcium appears to be one of the primary materials in the soil which limit the distribution of land snails.

The first area, surveyed June 27, is a northwest-facing, unshaded prairie wash located in B4. This wash contains medium to large limestone rocks on a gradual slope. Prairie grasses surround the rocks, and numerous snails were found among the roots which were exposed when the rocks were overturned. The soil under the rocks was moist and the wash drains into a roadside ditch. The potassium content was low at this station (Table II). This limestone habitat yielded only three species in any abundance. The 639 *Gastrocopta armifera* represented the largest number of individuals of one species taken at one station. *Pupoides albilabris* was more abundant here than at any other station and *Gastrocopta procera* was also common.

A second limestone outcrop is an abandoned rock quarry on a ridge in B39, which was surveyed June 29. A depression in the area about 50 feet in diameter is surrounded by very large limestone rocks. Winter and early spring precipitation accumulates in the depression (Hartman, 1960); however, on the date of the survey the soil was very dry. There was evidence of heavy trampling by cattle in the depression, and vegetation is very scanty. Towards the periphery and outside of the depression there are clumps of big bluestem, switchgrass *(Panicum virgatum)*, barnyard grass *(Echinocloa crusgalli)*, and wild rye *(Elymus canadensis)*. The percentage of organic matter was low at this area (Table II). No living snails were found in the quarry. However, 209 shells of *Lymnaea bulimoides techella* were found mainly under the smaller limestone rocks. No other species were found in the depression area; however, a few others were taken from under the small rocks surrounding the quarry.

The third limestone outcrop, surveyed July 6, is a south-facing, unshaded habitat in D7 (Fig. 1). There were many small to medium sized limestone rocks and the soil underneath was very dry. The ground was trampled and the area heavily grazed. The grasses were cut off at the roots and could not be identified. Some of the common plants in the area were leadplant *(Amorpha canescens)*, ironweed, silverleaf scurfpea *(Psoralea agrophyla)*, black sampson *(Echinacea pallida)*, and thistle *(Cirsium altissimum)*. The organic matter was high compared to the other areas (Table II). Only three species were collected here: *Pupoides albilabris*, *Gastrocopta armifera*, and *G. procera* (Table II). All were fairly abundant and represented only by dead shells.

The fourth limestone area is a heavily shaded ledge in a wooded area along both sides of a stream in C33. This region was surveyed July 15. There is a fairly sharp slope from the ledge to the creek and smaller limestone rocks are found on this slope. The ledge runs east and west, and it was noted that there were many more snails on the north-facing ledge. Some of the dominant vegetation in the area is black locust *(Robinia pseudoacacia)*, honey locust, osage orange, smooth and fragrant sumac, dogwood, hackberry, American Elm, green ash, and black walnut. The ground cover is not lush. Several large limestone rocks in the ledges were overturned and the soil appeared to be rich and moist. The highest percentage of organic matter on the reservation was measured at this station. Over 56 per cent of the specimens collected were *Vallonia parvula* or *Gastrocopta armifera*. The largest population on the reservation of *V. parvula, Helicodiscus parallelus* and *Stenotrema leai aliciae* was taken at this station.

The last limestone outcrop, surveyed August 2, is in B26. The largest rocks on this west-facing slope were moist underneath and most of the shells were collected there. The dominant vegetation is little bluestem, side oats grama, silverleaf scurfpea, wild indigo *(Baptisia leucuphea)*, ironweed, leadplant, and patches of fragrant sumac. The lowest pH on the reservation was measured at this station and the organic content was high. Over 65 per cent of the specimens taken were *Gastrocopta armifera*. The largest population of *Gastrocopta procera* was taken at this station. The only other species taken in large numbers was *Pupoides albilabris*.

In general, *G. Armifera* was the most common snail in the unshaded limestone outcrops. *Pupoides albilabris* and *G. procera* were also well represented. The unique quarry presented a different situation. *Vallonia parvula* was prevalent in the shaded limestone outcrop.

PRAIRIE AREAS

Collections were made from four grazed, open prairie areas on the reservation. The areas surveyed were in A6, B35, B53, and B8. Hartman (1960) reports that little bluestem and Indian grass dominate the unbroken upland in the western two-thirds of the B section and the northern half of section D. The scattered, moderately grazed areas have a thinner cover of little bluestem, side-oats grama and tall dropseed *(Sporobolus asper)*. Denuded areas, ravines and broad washes were invaded by arrow-feather *(Aristida purpurascens)*, goosegrass *(Eleusine indica)*, Virginia wild rye *(Elymus virginicus)*, muhly *(Muhlenbergia brachyphylla)*, witch grass *(Panicum capillare)* and yellow bristle grass *(Setaria lutescens)*. Some of the more frequently occurring prairie vegetation noted during the summer were leadplant, ironweed, silverleaf scurfpea, thistle, common ragweed *(Ambrosia artemisiifolia)*, milkweed, yarrow (*Achillea millefolium*), daisy fleabane *(Erigeron ramosus)* and broomweed *(Gutierrezia dracunculoides)*. Most of the gastropods taken from the prairie areas were represented only by shells.

The A6 prairie area, surveyed June 21, has a thick cover of prairie vegetation. The area is flat and is in a region where the surface soil is described as moderately deep, dark, friable and silt to clay (Eikleberry, Fly, and Dodge, 1956). The pH at this station was 6.0, one of the most acid conditions on the reservation (Table II). Most of the specimens taken at this station were collected under cow dung. Limestone rocks were very scarce. Five species were taken at this station. *Gastrocopta armifera* was common and comprised over 78 per cent of the collection. *Pupoides albilabris, Gastrocopta procera,* and *Helicodiscus parallelus* were sparsely represented at this station.

The B35 area, surveyed July 1, is on a gradual, northwest-facing slope next to the crest of a hill. It was described as being in the same soil region as A6 (Eikleberry, Fly, and Dodge, 1956). A few limestone rocks are present and a thicket of smooth sumac is on the north end of the collection area. The soil pH was 6.2 and the nitrogen content was high compared to that of the other stations. *Gastrocopta procera, Pupoides albilabris,* and *Helicodiscus parallelus* were sparsely represented at this station.

Prairie area B53, surveyed July 13, is on a gradual, south-facing slope. Limestone rocks and dung piles are scarce at this station. This area has a fairly thick cover of prairie vegetation. Only 21 specimens were taken from this area.

Area B8, surveyed August 4, has more limestone rocks and dung piles than any other prairie area. The surface soils are light brown and are three to five inches deep with gravel or chert subsoils (Eikelberry, Fly, and Dodge, 1956). The soil is acid in this prairie area (Table II). Only three species were collected. *Gastrocopta armifera* comprised almost 83 per cent of the collection. *Pupoides albilabris* and *Gastrocopta procera* were the other two species collected.

The soil pH at the prairie areas was acid. Burch (1955) stated that pH has little influence and is not a limiting factor in the distribution of snails. In general, *G. armifera, G. procera,* and *P. albilabris* were the most abundant snails in the prairie. In the grazed meadow on the University of Kansas Reservation, Leonard and Goble (1952) found only *G. armifera, G. procera,* and *Bulimulus dealbatus,* and all of these were rare.

ACCOUNTS OF SPECIES

Physa hawnii Lea

This midwestern species is found in the eastern third of Kansas with scattered records farther west. *P. hawnii,* a typical pond snail, is one of the most common aquatic gastropods in Kansas, and is found in roadside ditches, streams, lakes, and rivers. Most of the specimens were found on rocks and dead sticks just under the surface of the water in the ponds (B48, A5) and the stream (B48, A21), while a few were taken from the stems of aquatic plants. Although very common at the aquatic stations on the reservation, a few shells were

TABLE III.—Distribution of molluscan species according to habitat on the Ross Natural History Reservation (the numbers represent the number of each species collected at each area)

	Stream (B48-A21)	Gladfelter pond (B48)	Ponds (A5)	Spring (A39)	Rotten log (C33)	Wooded area (C33)	Wooded area (A21)	Hedgerow (A42-39)	Hedgerow (B1-16)	Abandoned farmsite (C63)	Prairie wash (B4)	Abandoned quarry (B26)	South-facing slope (D7)	Limestone ledge (C33)	West-facing slope (B26)	Prairie (A6)	Prairie (B35)	Prairie (B53)	Prairie (B8)
Physa hawnii	498	132	70	1						19									
Helisoma trivolvis			44																
Lymnaea parva				10			1												
Lymnaea bulimoides	10	16	59						1			209			1				
Gastrocopta armifera	1	3		135		76	188	251	147	9	639	15	78	69	382	78			126
Gastrocopta contracta				10			36	7						9	23				
Gastrocopta pentodon								2											
Gastrocopta procera				8		2	6		5		42	8	71	20	109	7	12	7	15
Gastrocopta cristata							1												
Gastrocopta tappaniana				10			9												
Pupoides albilabris				38		18	14	5	10	1	103	1	89	31	46	10	8	10	11
Succinea sp.	9	34	3	86	11	24	12	1	23	2				5	8	2		2	
Vallonia parvula				72		15	103	71	153	2				106	7				
Helicodiscus parallelus		1					1	3						25					
Helicodiscus singleyanus									1							2		2	
Stenotrema leai aliciae					4	12		12						25	1				
Bulimulus dealbatus			3																
Hawaiia minuscula				19			14				1			5	5		4		
Retinella indentata	2			32			12	59											
Zonitoides arboreus	3			2	191	47	64	21						16					
Sphaerium sp.			28																
Uniomerus tetralasmus			3																

taken from the clay basement of an abandoned homestead in C63 which probably contained water during much of the year.

Fifty individuals from the stream were checked for trematode parasites. One was found to be infected with a fluke of the Xiphidiocercaria group.

Helisoma trivolvis lentum (Say)

This species, common throughout Kansas and much of eastern North America, inhabits rivers, small streams, lakes, ponds, and roadside ditches. Large colonies are often found in quiet, more or less stagnant, shallow water on ooze-covered bottoms and on rocks and dead plants. Alice Leonard (1943) finds that it can survive long periods of drought, apparently by burrowing into the mud at the bottoms of drying pools.

Helisoma trivolvis lentum was found at one station on the reservation, the smaller of the two ponds in A5. Forty-four specimens, most of them living, were taken from the rocks, sticks, and mud bottom of the pond.

Lymnaea parva Lea

Widely distributed east of the Rockies, this snail is found primarily in the eastern half in Kansas. It is rarely found in water although it does require a rather moist habitat, often living on sticks, stones, or mud flats on exposed mud bottoms of transient pools and on moist drift along stream banks.

Lymnaea parva was not common on the reservation and was collected at only two stations, the spring (A39) and the wooded area (A21). Dead shells were found under limestone rocks around the spring and under small logs in the wooded area.

Lymnaea bulimoides techella (Haldeman)

In contrast to the three species just discussed, this is primarily a southwestern form, extending into northern Mexico (Baker, 1911). The study area is near the northeastern limit of distribution of this species, and in this case represents an area of overlap between elements characteristic of southern and northern faunas.

Lymnaea bulimoides techella often may be found in ephemeral pools where it appears in large numbers for a few weeks in early spring. Few adults are seen through the hot summer months (Franzen and Leonard, 1943). It commonly lives in shallow water with a mud or ooze-covered bottom. In Franklin County, Kansas, it was found living in a large rock quarry at the edges of several shallow pools, by Leonard (1955).

Many dead shells were collected from a depression in the abandoned quarry (B26) on the reservation. The depression was dry at the time of the collection, but it usually contains a small pool of water. Living specimens were taken from rocks and plants on the edges of the ponds (B48, A5) and dead shells were recovered by screening mud and gravel from the bottom of the ponds and the

stream (B48-A21). Although this species was collected at six stations, the quarry (B26) was the only one containing great numbers of shells.

Gastrocopta armifera (Say)

Leonard and Goble (1952) list this wide-ranging species as common throughout Kansas. Although Baker (1939) notes that this is a characteristic snail of prairie regions, preferring dry habitats, we found that it was most abundant in moister areas where there were many limestone rocks. Franzen and Leonard (1947) state that in prolonged dry, hot summer months *G. armifera* is able to aestivate, making possible its survival in Kansas. However, two of the three collections in which this species did not occur were from open prairie areas (B35, B53), indicating that conditions there may be too severe even for this tolerant form. Archer (1937) finds *G. armifera* to be rare or absent in woods, but our study indicates that the species may be found there, confirming the observations of Alice Leonard (1943).

This is the most common snail on the reservation; it was collected at 13 of 16 terrestrial stations. It was extremely abundant in the dry bed of a prairie wash gully in section B4, where 639 specimens were taken, 261 of which were under a single rock. Many specimens were also found in rotten log and leaf litter in wooded areas, and a few were turned up under cow dung.

Gastrocopta contracta (Say)

In Kansas, *G. contracta* is found primarily in the eastern half of the state; it is also recorded from Canada, Mexico, and many areas in the United States. This snail occupies almost as wide a variety of habitats as *Gastrocopta armifera*, but does not seem to be as abundant at any given locality. Its usual habitat is on shaded slopes along watercourses under dead wood, leaf mold, and grass (Franzen and Leonard, 1947). It exhibits a well defined preference for mesic habitats, but also occurs in relatively dry places (Fitch and Lokke, 1956).

In their survey, Leonard and Goble (1952) found *G. contracta* at six of eight terrestrial stations, but nowhere was it abundant.

Gastrocopta contracta was collected in relatively small numbers at 5 of 16 terrestrial stations on the Ross Reservation. Specimens were taken from a west-facing slope (B26), limestone ledge (C33), spring area (A39), and wooded slope (A21). Most of the shells occurred under rocks in fairly moist conditions or under leaf mold in shaded areas. A few dead shells were recovered from screenings of debris from the limestone ledge.

Gastrocopta pentodon (Say)

This species occurs in wooded areas and under suitable cover in grasslands (Leonard, 1959). Baker (1939) states that it is seldom found in wet places. In Kansas, it is found in the southeastern portion; the range of the species in America is from Canada southward to Guatemala.

Two dead shells found in leaf litter in a hedgerow (A42-A39) were the only individuals of this species collected on the reservation.

Gastrocopta procera (Gould)

G. procera is an eastern American species, common in all but the extreme western counties of Kansas. It seems to be able to survive more adverse conditions than many other gastropods in the state. Leonard and Goble (1952) believe that the success of this species in Kansas is due to its ability to withstand periods of drought and high temperature. It favors hillsides and shuns extremely moist situations. Favorable habitats include timbered areas, both in upland and flood-plain situations, as well as grasslands (Leonard, 1959), and it is frequently found beneath leaves and about old logs (Baker, 1939).

This was one of the most common snails on the reservation, collected at 13 of the 16 terrestrial stations. It seemed to be most abundant on the west-facing slope (B26) where 109 specimens were recovered. This was one of the shells commonly found in dry conditions on the open prairie, and was frequently associated with ***Pupoides albilabris***. *G. procera* seemed to favor fairly dry environments since it was not abundant in the more mesic areas of the hedgerows and woods. Shells were generally collected under limestone rocks and cow dung, although many were found buried among the roots of prairie grasses.

Gastrocopta cristata (Pilsbry and Vanatta)

This snail is usually found associated with *G. procera* on timbered slopes near streams (Franzen and Leonard, 1947). One dead shell, probably of this species, was collected in the woods area in A21. The shell lacked the bifid lamellae of typical *G. procera* although there is a possibility that it was an immature specimen.

Gastrocopta tappaniana (C. B. Adams)

This common Kansas snail is found over much of eastern North America with the exception of the southern Atlantic coast states. Its most frequent habitat is on shaded slopes near streams (Franzen and Leonard, 1947). Both Baker (1939) and Leonard (1959) list favorable habitats for *G. tappaniana* as pieces of wood, logs, and damp debris in moist places.

Ten shells of this species were collected under rocks around the spring (A39), and nine dead shells were collected under decaying logs in the wooded area of A21.

Pupoides albilabris (C. B. Adams)

This widely distributed snail is found over much of the state although records are lacking for the extreme western counties. Like *Gastrocopta procera,* with which it is frequently associated, ***P. albilabris*** seems to be adaptable to a variety of conditions. Although Archer (1939) writes that this species apparently does not occur in woodland

cover, Leonard and Goble (1952) report that it is found in woodlands as well as in open country. It lives under stones or at the roots of grass in well drained but often sunny places. Following rains it is sometimes found a few feet from the ground on trees (Pilsbry, 1948). Leonard (1959) finds *P. albilabris* tolerant to arid conditions and high temperatures and says it is often found under sticks, logs, and litter in wooded areas, as well as in drier situations such as open pastures. Its common habitats include wooded bluffs and hillsides by rivers and streams (Baker, 1939).

We found this species to be the most widely distributed snail on the reservation, but it was not as abundant as *Gastrocopta armifera* or *Vallonia parvula*. It was collected at 15 of 16 terrestrial stations with the largest number of individuals being found under limestone rocks in a prairie wash (B4). This was the most common snail in extremely dry conditions on the open prairie, often occurring among the roots of grasses.

Succinea sp.

This family is worldwide in distribution with species most numerous in America, southern Asia, Hawaii, and Europe. The usual habitat of the genus is on plants growing in or near the water (Leonard and Goble, 1952).

Succinea occurred over most of the reservation. Fourteen different collection areas provided shells of this snail, although most of them were dead. Reeds and grasses near or in the water at the spring and the undersides of rotting logs and leaf litter were the best collecting areas.

Vallonia parvula (Sterki)

According to Taylor (1960), this species occurs on the Great Plains from South Dakota to north-central Oklahoma; eastward to northern Missouri, northern Ohio, southern Ontario, and western New York. The species is generally distributed over Kansas, but is absent from the southwestern counties.

Most surveys indicate the *V. parvula prefers woodlands*. Leonard (1959) gave wooded areas in upland and floodplain situations as favorable localities. Baker (1939) found the habitat to vary from woodlands adjoining small lakes to bluffs of rivers, while Franzen and Leonard (1943) reported this species as occurring under logs or stones where there is considerable moisture, although it will survive arid periods. In northern Nebraska, *Vallonia parvula* occurs under logs, bark, and stones on slightly moist leaf mold in wooded areas (Taylor, 1960). A Leonard (1943) characterizes this snail as highly successful in the arid conditions of western Kansas.

The Ross Reservation survey tended to verify the above observations. *Vallonia parvula* was collected at 8 of 16 terrestrial stations, but was completely absent on the prairie and other extremely dry areas. Most of the shells were collected in hedgerows (B1-B16) and under the limestone ledge (C33). Shells were usually collected in loose leaf

mold and in soil under hedgerows and limestone outcrops, athough a few were found under rocks.

Helicodiscus parallelus (Say)

This species occurs in Kansas as far west as Meade County (Leonard and Goble, 1952), and also over much of the northeastern United States. This is a forest snail living on decaying wood or damp leaves in shady or humid places (Pilsbry, 1948). Its most natural habitat is in wooded river valleys or in floodplain areas (Baker, 1939). In more arid parts of the state of Kansas this snail is limited to woodland cover and usually occurs in decaying timber (Leonard and Goble, 1952).

Only dead shells of this species were collected on the reservation. Several badly weathered shells were found in loose soil under the limestone ledge (C33) and most of the other shells came from debris and leaf litter in the hedgerow (A42-A39) and the wooded area (A21).

Helicodiscus singleyanus singleyanus (Pilsbry)

An eastern American species, this snail is generally distributed over the eastern two-thirds of Kansas. It has apparently never been collected alive in the High Plains. In southwestern Kansas fresh shells have been found by University of Michigan field parties in the course of collecting fossils by washing matrix through screens. It seems probable that *H. singleyanus* lives among grass roots, even on exposed slopes that become hot and dry during the summer (Taylor, 1960). It is usually found under forest debris or among leaves or piles of washed materials (Baker, 1939).

Only four specimens were collected in this study. These shells, all dead, came from siftings of debris and loose soil in the wooded area (C33), hedgerow (B1-B16), and prairie area (A6).

Stenotrema leai aliciae (Pilsbry)

At the present time this species is limited to the eastern section of Kansas. It forms part of a series of closely intergrading forms found over much of eastern North America. Leonard (1959), Leonard and Goble (1952) and Pilsbry (1940) record this snail as an inhabitant of moist or very humid areas. Franzen and Leonard (1943) write of it as distinctly a woodland snail in northeastern Kansas.

Our findings tend to substantiate these statements. In all cases, this species was collected on the reservation in wooded or shaded areas having a fair amount of moisture. It was most common around the limestone ledge in C33, but was not abundant anywhere. At the five stations where this species was collected, shells were found under decaying logs, in leaf mold and in other decaying plant parts.

Bulimulus dealbatus (Say)

Our study area is near the northeastern limit of distribution for this tropical American family. *B. dealbatus* is a colonial snail, usually

found in open, arid country. Populations usually occur on summit areas, often on bluffs along rivers, and hibernate by burrowing in soil (Leonard and Goble, 1952).

Only three dead shells of this species were found on the reservation. These were collected on the dam of a small pond in A5. We are not sure how they got there.

Hawaiia minuscula minuscula (Binney)

This small mollusk has followed the paths of man throughout much of the world. Although it can withstand arid conditions, it is most abundant in wooded places where moisture conditions are better than on the treeless prairies (A. Leonard, 1943). Baker (1939) and Leonard and Goble (1952) also named wooded areas as the most favorable habitat for this species. The snail may be found under logs, sticks, stones and clumps of grass in floodplain and upland situations, and it seems to thrive in piles of moist drift that have been cast by floodwaters (Franzen and Leonard, 1943).

Although *H. minuscula* was not abundant on the reservation, it wase found in dry as well as in moist situations. The greatest number were collected under rocks around the spring (A39) and under logs in the wooded area (A21), but shells were also found on the relatively dry prairie (B35) and west-facing slope (B26). Specimens were usually found under rocks, logs, and loose soil at the collecting points.

Retinella indentata (Say)

This species is limited to the eastern third in Kansas, which marks its western boundary in North America. It is found along river valleys, in wooded areas and in former prairie lands (Baker, 1939), usually occurring on timbered slopes under stones, logs, loose bark, and debris. It is rare in open country, although it occurs on rocky slopes having sparse cover, according to Leonard and Goble (1952).

Fitch and Lokke (1952) found *Retinella indentata* well represented on the University of Kansas Natural History Reservation, but it was less abundant than *Retinella electrina* in moist woodlands. It is usually found associated with *Zonitoides arboreus* and *R. electrina* (Franzen and Leonard, 1943).

This species was not as common as *Zonitoides arboreus* on the Ross Reservation. It was found at three terrestrial stations, and two dead shells were taken from gravel screenings on the bottom of the stream (B48-A21). Here also, it was usually connected in conjunction with *Z. arboreus.* It was collected from moist areas only, with the largest number found under moist leaf mold in a hedgerow (A42-A39). This species was often found under or on rotting wood or in moist leaf litter.

Zonitoides arboreus (Say)

This snail has been introduced into many parts of the world, and is found over the North American continent. It is distributed over the eastern half of Kansas. Pilsbry (1946) found it to be abundant

wherever there were trees or shelter of any kind in the eastern states in the Mississippi valley. He stated that it can be found under bark, boards, bricks, or stones, or any like situation offering protection from the sun, with sufficient moisture. In northern Nebraska, it was found under logs and bark and among leaves on damp ground, usually in wooded areas (Taylor, 1960). Rotten wood is an ideal place for this species.

Zonitoides arboreus was found in the more humid areas on the reservation, including the spring (A39), the two wooded slopes, the hedgerow (A42-A39), and a rotten log. It was not found at any of the drier situations and was almost always collected under logs or sticks or other places where moisture was abundant. From one small rotten log, 191 specimens were taken.

Sphaerium sp.

This genus is found in rivers, ponds, and lakes, usually on the surface or buried at various depths in soft mud (Baker, 1928). In Kansas, *Sphaerium* is more commonly found in streams than in ponds (Leonard and Goble, 1952).

These small clams were found in the smaller of the two ponds in A5. A few living specimens were found on the mud bottom near the pond's edge and many dead shells were found around the edges of the pond.

Uniomerus tetralasmus (Ward)

This species is able to dig into the mud bottoms of ponds or streams to a depth of a foot or more and is thus able to "hibernate" during dry periods (Baker, 1928a). This is a common mussel in ponds and other water bodies in Kansas.

Three dead shells of this species were picked up on the edges of the larger of two ponds in A5. No living specimens were found.

CHECK LIST OF THE MOLLUSCA OF THE ROSS RESERVATION

Phylum Mollusca
- Class Gastropoda
  - Order Pulmonata
    - Suborder Basommatophora
      - Family Physidae
        - *Physa hawnii* Lea
      - Family Planorbidae
        - *Helisoma trivolvis lentum* (Say)
      - Family Lymnaeidae
        - *Lymnaea bulimoides techella* (Haldeman)
    - Suborder Stylommatophora
      - Family Pupillidae
        - *Gastrocopta armifera* (Say)
        - *Gastrocopta contracta* (Say)
        - *Gastrocopta pentodon* (Say)
        - *Gastrocopta procera* (Gould)
        - *Gastrocopta cristata* (Pilsbry and Vanatta)

Gastrocopta tappaniana (C. B. Adams)
Pupoides albilabris (C. B. Adams)
Family Succineidae
Succinea sp.
Family Valloniidae
Vallonia parvula Sterki
Family Endodontidae
Helicodiscus parallelus (Say)
Helicodiscus singleyanus singleyanus (Pilsbry)
Family Polygyridae
Stenotrema leai aliciae (Pilsbry)
Family Bulimulidae
Bulimulus dealbatus (Say)
Family Zonitidae
Hawaiia minuscula minuscula (Binney)
Retinella indentata (Say)
Zonitoides arboreus (Say)
Class Lamellibranchia
Order Schizodonta
Family Unionidae
Uniomerus tetralasmus (Ward)
Order Heterodonta
Family Sphaereiidae
Sphaerium sp.

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Indication of the Sense of Smell in the Turkey Vulture, Cathartes aura (Linnaeus), from Feeding Tests

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ABSTRACT: Two turkey vultures, *Cathartes aura* (Linnaeus), were employed in a series of feeding trials. Birds were presented individually with leaf-filled pans in one of which meat was concealed from view. Pans were presented in the open, concealed from direct view behind screens, or concealed in boxes with single openings. In each type of feeding trial pans with food were selected first a significant number of times. Evidence of a sense of smell is believed afforded. Interpretations of results suggest that smell may be of a degree of importance varying with the situation confronting the bird. Preference for freshly-killed chicks over other types of fresh and decaying meat was shown. Various observations of the behavior of the captive birds are included.

Importance of the olfactory sense in the orientation of feeding activities of birds is poorly understood. Relative importance of the exteroceptors functional in food-finding by carrion-eating birds has long been of particular question. There seems to be little, if any, conclusive evidence that a sense of smell even exists in such species. The purpose of this investigation was to determine by means of feeding experiments whether a sense of smell could be demonstrated to exist in the Turkey Vulture, *Cathartes aura* (Linnaeus).

Literature pertaining to the possibility of olfaction in the Turkey Vulture or other species of the family Cathartidae is considerable. Many of the references are confusing or of questionable scientific value. Audubon (1859: 15), Darwin (1860: 175-176), and others presented negative evidence or rejected the possibility altogether. Beebe (1909: 467) gave conflicting evidence. Indications of a sense of smell have been given by Rhoades (1883), Gurney (1922: 241), and Howell (1932: 162). Strong (1911) indicated an intact well-developed olfactory nervous system in the Turkey Vulture. Northington (1936), however, has pointed out that the functional capacity of a sensory nerve may not be proportional to the size of the associated structure.

Two Turkey Vultures, sex undetermined, were trapped alive in Dade County, Florida, during the fall of 1953. They were housed in individual compartments consisting of an outer portion measuring 5′ x 5′ x 8′ in height, screened to the outside and provided with two perches each approximately six feet long, and a continuous inner portion of solid walls and ceiling, with dimensions of 9′ x 8′ x 8′. A door provided with one-way vision mirror-glass was situated in the far wall of each inner compartment.

After a period of eight weeks conditioning to confinement, controlled feeding was initiated. Canned dog food (largely horse meat),

which was allowed to putrify, was used in most feeding trials. Hatchery-obtained chicken culls, both freshly killed, and putrified, were also used.

Four types of feeding experiments were carried out. Observations of the birds after feeding pans were in position were made from outside the compartments through the mirror-glass.

Feeding experiment one.—Two identical metal pans were placed three feet apart in the center of each inner compartment. Both pans were filled with several inches of fresh dead leaves; putrescent horse meat was concealed beneath the leaves of one of the pans. In this and other experiments, relative positions of the food pans in successive feedings were rotated at random. Conditions permitting, feeding trials were made each day.

Feeding experiment two.—Two pans, which were placed approximately eight feet apart on opposite sides of the inner compartment, were concealed from direct view of the vultures by wooden screens. At the disturbance caused by placing the pans, the vultures invariably retreated to their perches. To reach the pans the birds were then obliged to pass the length of both compartments, go to one side of the inner compartment, walk around the screen and approach the pan from the side or rear. Pans were filled with dead leaves; putrescent horse meat was concealed in one of them.

Feeding experiment three.—Putrifying horse meat smeared on dead chicks was concealed in one of three identical, leaf-filled pans. Pans were placed two feet apart in line in the center of the inner compartment.

Feeding experiment four.—Each of three leaf-filled pans was placed in a wooden box provided with a three-inch diameter opening. Boxes were identical and were placed in a line, approximately two feet apart; the openings faced in the opposite direction from which the vultures approached them. The birds were obliged to thrust their heads through the opening and explore the leaf-filled pans for horse meat-smeared chick-culls.

The vultures usually hopped from their perches and approached the feeding setups within a few minutes after the disturbances incidental to pan-placing. In some instances the birds were slow to, or did not initiate food investigation during the observation period. Such instances are reflected in the data of Table I.

The initial impulse to seek food was probably a conditioned reaction involving auditory and visual stimuli connected with placing the food pans in position; in no case did this impulse arise, necessarily, from olfactory stimulation.

RESULTS AND DISCUSSION

Data obtained from the feeding experiments is expressed in Table I. These results furnish indication that the Turkey Vulture does possess a sense of smell. Results of Experiments One and Two are statistically significant. In Experiments Three and Four, x^2 values in

the case of Vulture I, which exhibited the smallest number of correct choices, are 18.0 and 9.4; the probability (two degrees of freedom) of these feeding choices occurring by chance is less than .01 per cent.

It is to be emphasized that no attempt has been made to ascertain the importance of smell to the Turkey Vulture in locating food under natural conditions.

The functional organization of the nervous system provides a resultant response to a correlation of perceptions from stimuli of the special senses. In situations where certain perceptions are of relatively great importance to the organism, a minimal stimulus may be utilized to its fullest measure. In the Turkey Vulture, for example, the visual sense may suffice to insure the finding of food. But under varying

TABLE I.—Results of feeding experiments with two Turkey Vultures

	EXPERIMENT 1			EXPERIMENT 2		
	Bird		Total	Bird		Total
	1	2		1	2	
Number of trials	47	47	94	42	42	84
Number of trials during which feeding was begun	32	28	60	22	38	60
Number of times pan with food was investigated first	30	21	51	21	36	57
Percent of number of observed feedings in which pan with food was investigated first	93	75	84	95	94	94
Number of times pan(s) without food was (were) investigated first	2	7	9	1	2	3
Percent of number of observed feedings in which pan(s) without food was (were) investigated first	6	25	16	4	6	5
	EXPERIMENT 3			EXPERIMENT 4		
	Bird		Total	Bird		Total
	1	2		1	2	
Number of trials	55	55	110	45	45	90
Number of trials during which feeding was begun	44	46	90	44	45	89
Number of times pan with food was investigated first	28	30	58	24	27	51
Percent of number of observed feedings in which pan with food was investigated first	63	65	64	54	60	57
Number of times pan(s) without food was (were) investigated first	16	16	32	21	18	39
Percent of number of observed feedings in which pan(s) without food was (were) investigated first	36	34	35	46	40	43

situations other senses may attain prominence. Thus in certain situations the sense of smell may be of importance to the bird. In this respect the results of Experiment Two, in which the greatest number of correct choices was made by both birds, are interesting. Here pans were situated at the compartments' ends which were shunned by the birds because they contained the doors through which the investigators entered. Approach to a pan as well as escape from its vicinity was possible from but one direction. The birds' great timidity may well have resulted in greater discrimination on their part.

A sense of smell in the Turkey Vulture might also function in selection of carcasses as well as portions of a carcass. Hamrum (1953: 877) found indications that odor (and taste) may influence the food choice of the Bobwhite, *Colinus virginianus* (Linn.).

The smallest number of correct choices was made in Experiment Four, in which the pans were concealed within wooden boxes. It is not improbable that the normal diffusion of food odor was impeded by the box. Diminished olfactory stimulation may have resulted in a greater degree of exploration for food.

It may be questioned if use of but two birds affords results which are to be regarded as representative of the species. General behavior of the birds was considerably stereotyped. There is considerable uniformity in statistical comparison of their choices.

ADDITIONAL OBSERVATIONS

The vultures appeared to be in good health throughout their 18 months of confinement. However, they made little adjustment to captivity. Their escape tactics never ceased. When presence of people was realized, the birds remained poised for retreat. Constant flapping against the screen walls resulted in frayed remiges and rectrices. Water consumption appeared to be negligible; only once was a bird observed to drink. On no occasion was it observed that undigested material was regurgitated in pellet form. Frightened birds usually regurgitated any food recently taken; in most cases this was soon re-eaten.

Both vultures continuously explored their quarters and any strange objects within them. Brooms, paper cartons, pieces of paper and other materials left in the cages were scattered about and often torn to bits. Having fed, the birds would tear the leaves from the foodless pans. In this respect, attention should be called to various trials which have been made with confined vultures in which nonodorous models of animals have been employed.

The avidity of the vultures for freshly-killed chicks invited a series of feeding trials in which a choice of meats, as well as the degree of decomposition of such, could be made. A single pan with exposed food in each of its corners was presented to the birds. Food was arranged as follows: corner A, fresh canned horse meat; corner B, odorous, decaying horse meat; corner C, freshly killed chick; corner D, freshly-killed chicks smeared with odorous, decaying horse meat. Sixty

observations (thirty for each bird) were made as to the food selected first. The freshly-killed chick was selected first 45 times; the freshly-killed chick smeared with putrifying horse meat was selected first 13 times; the fresh horse meat was selected first two times; the putrifying horse meat was never selected first. A preference for fresh meat as well as a type of fresh meat, was thus indicated. This being the case, the question may well be raised concerning the use of a sense of smell in locating freshly-killed, presumably relatively nonodorous materials under natural conditions. It also suggests that a diet of carrion may, under natural conditions, not be preferential.

There are reports of Turkey Vultures attacking live animals. Hamilton (1941) noted attacks on newly born pigs, and Wayne (1910: 67) reported that they picked the eyes from a live, but mired cow or horse. Parmalee (1954: 443), reporting on depredations by vultures in Texas, concluded that most, if not all, of the live domestic animals preyed upon by vultures were attacked by Black Vultures. He pointed out that reports of similar attacks by Turkey Vultures may be based upon mistaken identification. When live chicks were released in our captive vultures' compartments, the vultures immediately retreated, although they had had much experience in feeding on dead ones. One vulture, starting to devour a dying chick, dropped it and trotted away in haste when the chick suddenly struggled.

The long-recognized importance in food location of visual cues afforded by the behavior of other vultures, as described by Meinertzhagen (1959: 127) and many others, was emphasized at the release of the captive birds at the termination of the feeding trials. Release was made on a cloudless morning at the edge of a large, unused landing mat for lighter-than-air-craft. No vultures had been observed in the vicinity. The first releasee flapped to a height of less than 50 feet and then glided to a landing approximately 100 yards distant. Within five minutes other vultures, both Turkey and Black, appeared in the area; seven were counted spiralling overhead. Three of the latter landed next to the releasee and spent several minutes walking about him. The second bird was now released. It flapped and glided to a landing approximately one mile distant. It was followed by the entire group of vultures which had gathered about the first releasee. Several of the birds landed near the second releasee and remained walking slowly about it.

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Population Structure and Reproduction in the Lizard Uta stansburiana stejnegeri

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ABSTRACT: Three populations of the lizard *Uta stansburiana stejnegeri* in western Texas were studied by mass sampling over a two-year period. Additional information was obtained by marking experiments in one of the populations.

The sex ratio is not significantly different from 50:50 in any population, age group or season. However, since males reach a larger size than females, samples containing predominantly large lizards may be as much as 90 per cent male.

All lizards mature at the age of one year or less. Despite differences in climatic conditions and other factors almost all lizards are reproductive during the mating season. There is an annual turnover in the population as most adults disappear at the end of their first reproductive season.

Reproductive potential is a function of size of the female and the season. Larger females produce larger clutches and clutch size is larger early in the reproductive season than later. Approximately 38 days are required from the beginning of ovarian follicle enlargement to ovulation; three clutches per year are laid by females maturing early in the season. Reproductive potential may be calculated accurately on the basis of number of oviducal eggs, number of yolk-filled follicles, or number of corpora lutea. Counts of total numbers of follicles are not useful for estimating reproductive potential.

Estimates of natality at the population level can be fairly accurately made by knowing the sizes of females in the population. This has been verified by field experiments.

Data are presented on ratio of juveniles to adults in the populations, on size and age at maturity, on testis development and regression, on corpora lutea and atretic follicles, on gonad development in juvenile lizards, seasonal cycles in the ovaries and interuterine migration of ova. Numerous comparisons are made with published data on other species of lizards.

Uta stansburiana stejnegeri, the desert side-blotched lizard is widely distributed in North America from Nevada and California to western Texas and northern Mexico (Smith, 1946). It is extremely abundant in western Texas and is more easily obtained in large numbers than most iguanid lizards. For these reasons it was chosen for sampling experiments to obtain data on reproductive cycles, population structure, and variation in morphological characteristics. The data on variation and stability of taxonomic characters will be published separately.

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counties in northwestern Texas and for his help on many field trips to that area. I am particularly grateful to Chester Rowell of Texas Technological College for his identification of certain plants.

INTRODUCTION AND DESCRIPTION OF AREAS

Many localities in northwestern and western Texas were investigated and three of these were chosen for sampling experiments. The most northerly population is at the northern extreme of the range of this lizard in Texas and lies in Palo Duro Canyon in extreme northern Armstrong County, 17 miles east southeast of Canyon, Texas. This canyon is a deep cut in the high plains of Texas with an altitude of about 3600 feet above sea level at the rim and 2000 feet or more on the canyon floor. The canyon has been cut by the aggrading Red River and, although quite rocky in places, has some considerable areas of riverborne sand on the floor. It is only in the sandy areas that *Uta stansburiana* is abundant; it does not show a preference for a rocky habitat anywhere in western Texas, but has been reported as saxicolous in some parts of its range by Smith (1946). The principal vegetation in the microhabitat is salt cedar (*Tamarix gallica*), sparse grasses, juniper, and cottonwoods along the permanent tributaries. Large piles of drift often provide a great deal of cover around the bases of these trees.

Other lizards occurring in the same habitat in order of apparent relative abundance are *Sceloporus undulatus consobrinus, Cnemidophorus tessellatus, Crotaphytus collaris collaris, Cnemidophorus sexlineatus, Phrynosoma cornutum* and *Eumeces obsoletus.*

The sampling area is characterized by hot summers, and winters during which conditions are alternately mild and rigorous. The summer temperatures are generally between 95° and 100°F; freezing occurs almost every night between November and early March. The mean July temperature is 78°F; the mean January temperature, 35°F and the length of the growing season 201 days.

The greatest difficulties in sampling were encountered in this northern population. Periodic flash rainstorms characteristic of this area of Texas send walls of water down the narrow canyon floor which often completely change the microhabitat, disrupting home ranges and washing away egg-laying sites. For this reason a second sampling area was chosen in Armstrong County on the Hedgecoke Ranch, 19 miles southwest of Claude. This second station is about 20 miles south of the first in a similar habitat. An extremely devastating flood in July, 1960, almost destroyed the lizard population at both stations.

The two southern study areas are 250 airline miles south of Armstrong County on the sandy mesquite plains at an altitude of about 2800 feet. One of the areas is located 6 miles south of Kermit, Winkler Co.; the other, 11.5 miles south of Monahans, Ward Co. The principal vegetation in both areas is a low shrubby mesquite (*Prosopis glandulosa*) with large intervening areas of loose sand supporting clumps of broom weed (*Xanthocephalum sarothrae*), sand

sage (*Artemisia filifolia*), allthorn (*Koberlinia spinosa*), huisache (*Mimosa* sp.) and beargrass (*Yucca angustifolia*).

The only other abundant lizards in these areas are *Cnemidophorus tigris, Phrynosoma cornutum* and *Crotaphytus wislizeni.*

The two southern populations are characterized by extremely hot summers and mild winters. The daily temperature in the summer is usually 100°F or higher. Sand temperatures taken daily in the summer at the Winkler County station were usually above 130°F with a difference of 60°F between maximum and minimum readings. The mean July temperature in the area is 82°; the mean January temperature, 46°; and the length of the growing season, 218 days.

Between the northern and two southern populations is a large area rather unfavorable for *Uta stansburiana* so that the northern population is partially isolated from the southern ones.

PROCEDURE

An attempt was made to get monthly samples from each of the three populations. This was possible in every month but December and January in the southern populations. Large samples were extremely difficult to obtain from the northern population at any time, but particularly during the winter. During the reproductive season in spring and summer, samples were collected more frequently. In all, 86 samples were collected; 33 from Armstrong County, 31 from Winkler County and 22 from Ward County.

Sampling was begun in the winter of 1958 and carried through the summer of 1960. A few samples were collected from the northern population prior to 1958 and the data from these specimens have been used in this paper where appropriate. In all, 416 specimens were obtained from Armstrong County, 616 from Ward County, and 875 from Winkler County, a total of 1907.

The specimens were usually preserved within four to six hours after capture. Sex in all lizards was determined by dissection although sex can be determined with a high degree of accuracy by the presence of enlarged postanal scales in males. Measurements of body length and of eggs or large ovarian follicles were made to the nearest millimeter with dividers while smaller follicles (5.0 mm or less)and all testes were measured to the nearest 0.1 mm with an ocular micrometer.

In addition to data obtained from samples, some important data on subjects discussed in this paper were obtained from marking experiments with *Uta stansburiana* in a 10,000 square yard quadrat area near the Winkler County sampling area. This marking study was begun as a part of a project studying the effects of radiation on a natural population of lizards supported by the U. S. Atomic Energy Commission.

POPULATION STRUCTURE

Sex Ratio

Sex could be determined in almost every specimen. Only in hatchlings that had been damaged internally was sex not determined.

Sex in adult lizards can be easily distinguished at a glance for there is strong sexual difference in pattern with the females being striped and drab, while males are unstriped and brightly colored with blues of various shades during the spring and summer. The ratio of all samples combined was 943 females to 945 males, almost exactly the expected 50:50.

The ratios are also not significantly different from 50:50 in any of the three populations. The percentage of 413 from Armstrong County was 49.4 per cent female; of 860 from Winkler County, 50.8 per cent female, and of 615 from Ward County, 49.1 per cent female. None of these data indicate that males are less easily captured than females because of a difference in habits as suggested by Smith (op. cit.), nor has this been my impression in the field.

The samples were also compared on the basis of season and of size groups of lizards. There are deviations from a 50:50 ratio in some of these seasonal groupings, but usually when the sample size is insufficiently large to be unbiased. Occasionally, deviations do occur in large samples, but these are still attributable to sampling errors. For example, during egg laying, females tend to stay near cover such as pack rat nests and males may thus be obtained in greater numbers.

The sex ratio at birth is difficult to ascertain from samples alone. The size at hatching is between 20 and 25 mm body length. The sex ratio of 126 lizards less than 30 mm and hence in their first few weeks of life is 52 per cent male, 48 per cent female. The ratio of 1009 known adults is 51 per cent male; 49 per cent female indicating close agreement and little ontogenetic change.

The sex ratio does change in different size groups of adults. This may be illustrated with the samples from Ward County. In the size group (arbitrarily selected) 41-50 mm there are 219 adult females and 116 adult males for a 65:35 ratio, while the ratio for 100 lizards in the group 51-60 mm is 6 females:94 males. The preponderance of males in the larger group is due to the fact that males attain a larger size than females. Note that the sex ratio of the total is 50:50.

Sex ratios of lizards marked in the Winkler County study area during the summer of 1960 may be indicative of the actual sex ratio. Of 111 juveniles marked in which sex could be determined with certainty, 59 were females and 52 males. Of the adults, 25 were females and 20 males. The difference in juveniles is insignificant, but is opposite to that obtained by sampling. The deviation from expectation in the adults is due to strong male rivalry in this species in which territories are discrete. Although another male will not be tolerated, one male may have more than a single female within his territory.

Ratio of Juveniles to Adults

For this comparison, the year was divided into four periods of three months each: January to March when females are developing large ovulatory follicles, April to June when most reproduction occurs, July through September when reproduction is completed and most

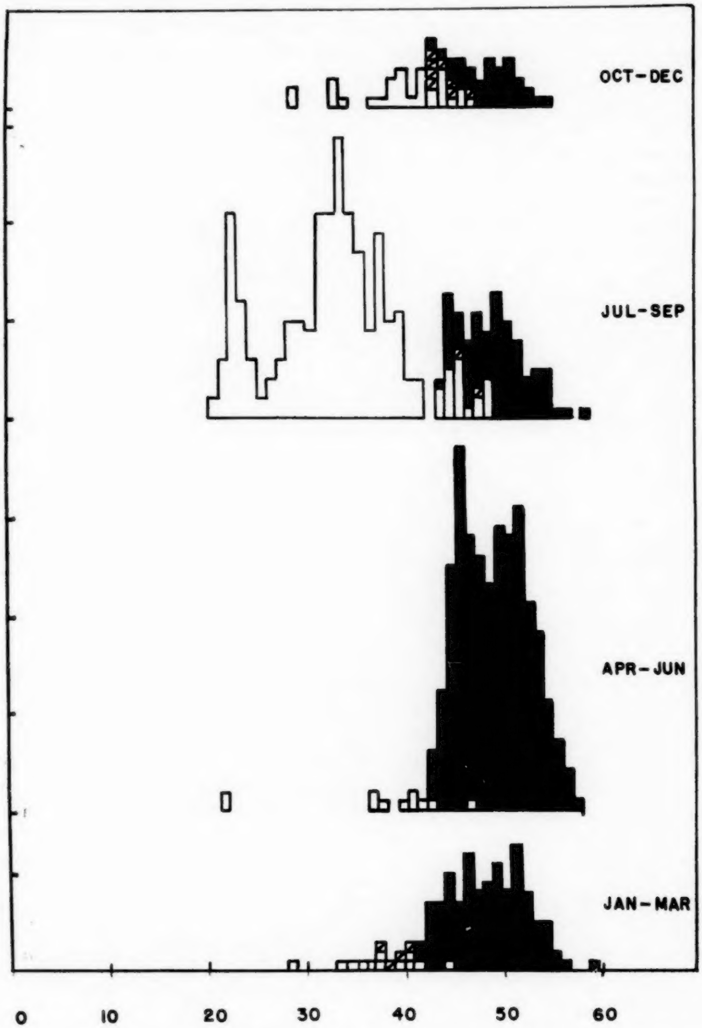

Fig. 1.—Histogram showing number of individuals of each size in *Uta stansburiana* in Winkler County, Texas, in four seasons. Abscissa: Body length in mm; ordinate: number of individuals. Each mark (other than those showing base lines) is 10 individuals.

hatchlings appear, and October to December when the gonads are quiescent and young lizards are reaching adult size. All periods, naturally overlap to some extent. The data for all years for which samples were available were combined. The distribution of size groups of lizards in each of these four periods is shown in Figures 1-3 and in different form in Table I.

It is apparent that most juveniles appear in all three populations in the period July to September with the peak number appearing in July and early August. The difference in the percentages of juveniles

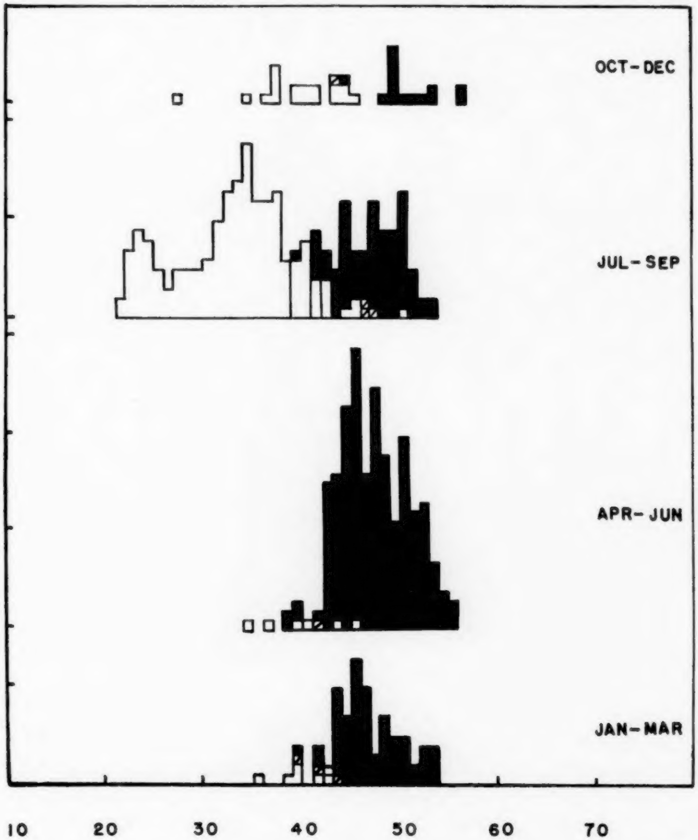

Fig. 2.—Histogram showing number of individuals of each size in *Uta stansburiana* in Ward County, Texas, in four seasons. Abscissa: Body length in mm; ordinate: number of individuals. Each mark (other than those showing base lines) is 10 individuals.

to adults during this period cannot be explained on the basis of available data.

Many of the juveniles reach mature size (40-45 mm) by the end of the summer during which they hatch. That some late season hatchlings were still quite small the following year is clear from the

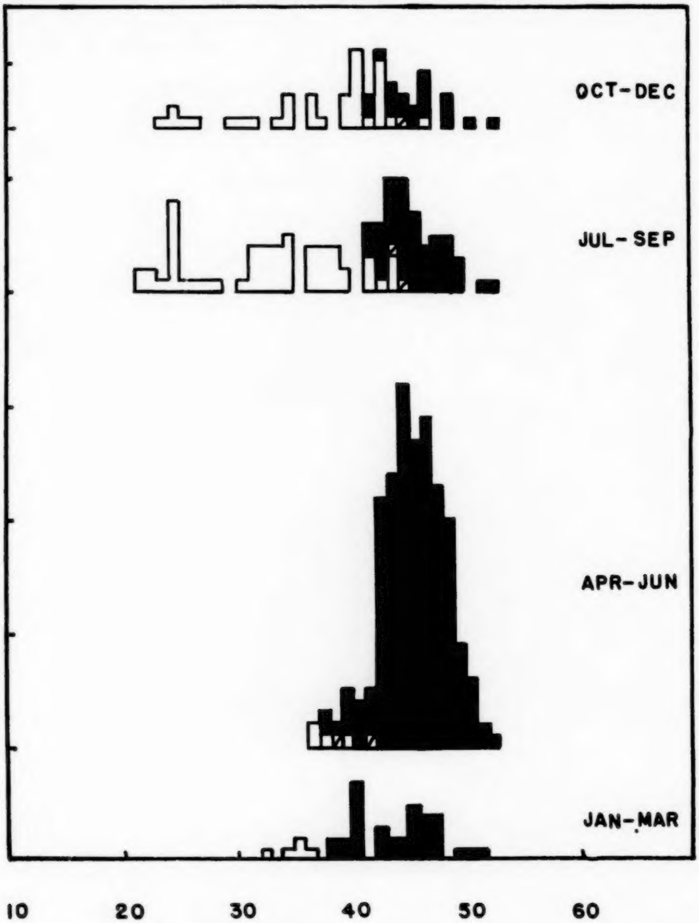

Fig. 3.—Histogram showing number of individuals of each size in *Uta stansburiana* in Armstrong County, Texas, in four seasons. Abscissa: Body length in mm; ordinate: number of individuals. Each mark (other than those showing base lines) is 10 individuals.

fact that there are lizards between 30 and 40 mm in length in each population in January-March. In fact, one specimen measuring only 22 mm was recorded in the Palo Duro population during this period. Such a small individual may have been hatched late the previous year and may not have grown at all the succeeding few months or it may have hatched from an egg that overwintered. The idea that many lizards reach adult size in the same summer they hatch has been verified by periodic measurements of marked hatchlings.

There is a greater percentage of juveniles in the October to December samples from Armstrong County than in the other two populations (Table I). This is what would be expected in the northern population because of its earlier winters and consequent shortening of the growing season. Too, hatching of the first clutch of eggs is probably generally later in the northern population than in the southern ones, so that few individuals can reach mature size by the end of the summer. This conclusion is substantiated by the figures that show a decrease in percentage of adults from July-September to October-December. If many juveniles were reaching mature size an increase should be expected in the later period and such an increase is evident in the Ward-Winkler populations.

The most significant point in these data is the indication that regardless of the relative percentages of adults and juveniles at any other season, almost all lizards in all three populations are mature in April-June, and the majority by January-March. These data demonstrate that nearly every lizard is potentially reproductive at an age of 10-12 months. Although some lizards mature only a few months after hatching, none will reproduce during their first season.

The relative percentages of mature and immature lizards in July-September must be discussed in greater detail. There is likely more error in these figures than in others because it is difficult to separate old adults from subadults hatched during that summer. Therefore,

TABLE I.—Percentages of juveniles and adults at different seasons in three populations of *Uta stansburiana* (figures do not add to 100 per cent because maturity could not be determined in some specimens)

	January-March		April-June		July-September		October-December	
	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults
Armstrong Co. N = 416	12.8	87.2	1.9	97.2	51.9	46.2	63.6	34.5
Winkler Co. N = 870	8.5	88.4	3.2	96.8	77.1	22.3	43.7	46.5
Ward Co. N = 604	7.3	89.0	2.3	96.4	66.9	32.0	52.9	44.1

the percentages of mature individuals may be too high. This possibility was investigated by comparing the number of adult lizards marked in a study area during June and July with the number of these "old" adults remaining in August and September. By mid-July every adult lizard in the study area had been marked and 23 of these were captured at least three times and must be considered residents of the area. By mid-August only 10 of these were still present in the area and in mid-September, only four. Areas adjacent to the study area were thoroughly investigated, but none of the lizards captured was marked. During the same period, the total number of lizards in the study area increased greatly and by mid-September some young lizards marked in June and July had reached or were nearing adult size. These data suggest a nearly complete annual turnover in the lizard population. Thus, data on relative abundance of juveniles and adults obtained from mass sampling during late summer and early fall are seen to be unreliable, at least if maturity is based upon criteria used by me and if there was not exceptionally greater mortality of marked lizards.

Size at Maturity, Average Size and Size Maxima

The females in all three populations may mature at a smaller size than males, but the difference in minimum size at maturity is a matter of only a few millimeters. It is easiest to be certain of maturity or immaturity during April-June because during this period yolk deposition, ovulation, or oviposition is occurring in females and enlargement of testes and vasa deferentia in males. Comparable data on sizes are shown below for the three populations:

	Minimum size at maturity	Average size of adults (April-June)	Maximum size of adults
Armstrong	38	45.9	53
Winkler	42	49.4	60
Ward	39	48.0	57

Although there are not great differences in these sizes, the smaller average size in the Armstrong County population reflects a rather striking difference in the distribution of size groups in this population. Most adults (91.7%) in the northern population are between 40 and 50 mm in body length while a smaller percentage is restricted to these limits in Winkler (59.4%) and Ward (70.5%) county populations. If there is an annual turnover of most adults in each population, this difference is to be expected because the shorter growing season in Armstrong County permits fewer individuals to reach the maximum size achieved by lizards in the other populations.

Most lizards studied reach sexual maturity rapidly, in many cases in the spring following birth the previous summer as is true in *Uta stansburiana*. Age at maturity has now been estimated in several species of North American lizards and these data are shown in Table II.

TABLE II.—Age at sexual maturity in 12 species of North American lizards

Species	Author	Age at Maturity (in years)
Cnemidophorus sexlineatus	Fitch (1958)	2
Cnemidophorus tigris	Tinkle (1959)	2-3-?
Anolis carolinensis	Gordon (1956)	1 or less
Holbrookia texana	Cagle (1950)	1
Sceloporus undulatus	Crenshaw (1955)	less than 1
Sceloporus olivaceus	Blair (1960)	1
Crotaphytus collaris	Fitch (1956)	2
Neoseps reynoldsi	Telford (1959)	1
Eumeces fasciatus	Fitch (1954)	2
Eumeces skiltonianus	Rodgers & Memmler (1943)	3
Eumeces septentrionalis	Breckenredge (1943)	in 3rd year
Eumeces obsoletus	Fitch (1955)	most 3; some 2

It can be seen that iguanid lizards studied mature within their first year, usually during their second growing season. Some may reach adult size the same year that they are hatched. The growth rate of scincid lizards is apparently slower and attainment of maturity is much slower despite the fact that as a group these species are not as large as the iguanids.

REPRODUCTIVE CYCLES

Counts and measurements of ovarian follicles of female lizards during each month have allowed formation of the composite descrip-

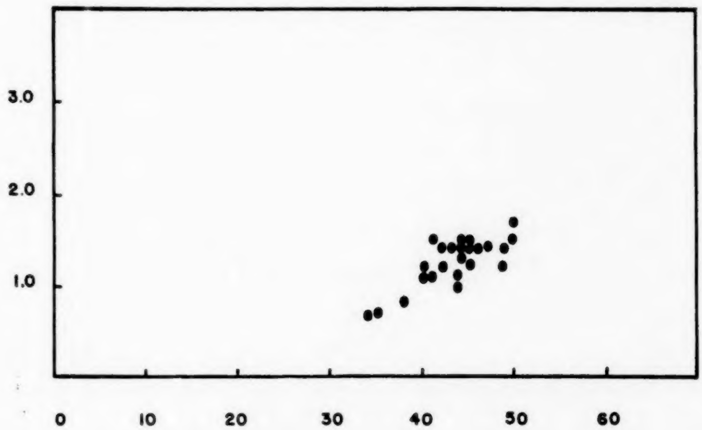

Fig. 4.—Size of largest follicles in ovary of *Uta stansburiana* in October to December. Abscissa: body length in mm; ordinate: size of follicles in millimeters.

tions of testis and ovarian development at each season. Unless otherwise stated all references are to adults. Since the development of the gonads is similar in each population and from year to year, the data in the graphs are of lizards from the Winkler County population obtained during 1959.

Winter Gonads (October to December; Figs. 4 and 5)

During this period, distinct size groups of follicles are not present in the ovary so that it cannot be said with certainty which follicles represent the first clutch for the following spring. The follicles are all pearly white or almost clear and the maximum size of follicles is 1.7 mm, but most of the largest ones are 1.5 mm or less and seldom less than 1.0. Miller (1948) reports that follicles in *Xantusia vigilis* are similar to those that I have reported in *Uta stansburiana* and are a maximum of 1.3 mm in diameter. However, according to Miller (1951) an ovum of this size has required two years to reach that

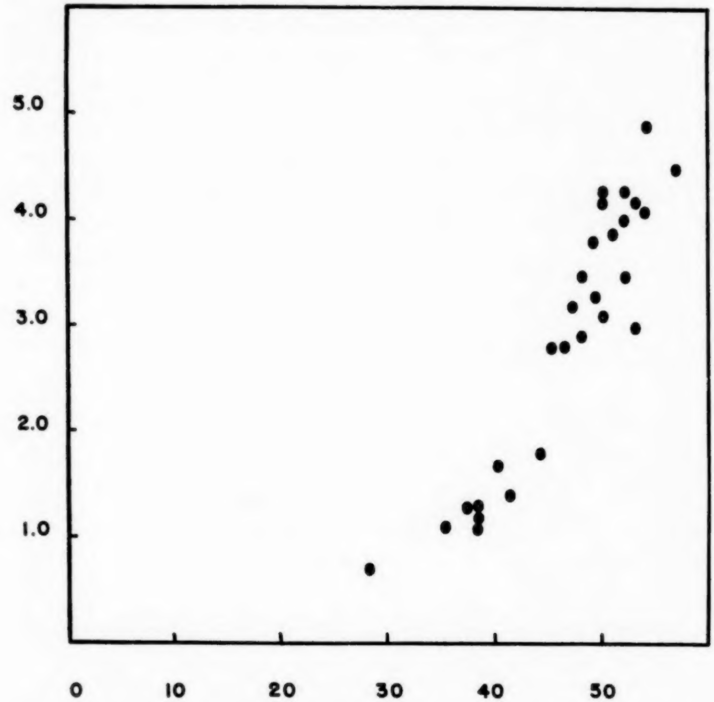

Fig. 5.—Maximum length of testis of *Uta stansburiana* in October to December. Abscissa: body length in mm; ordinate: size of testis in millimeters.

size and will require another to mature. Most of this in *Uta stansburiana* are 1.3 or less

The testes have generally undergone regression during this period with most being less than 4.0 mm in greatest length (maximum, 4.9 mm). The tubules of the testis are indistinct at this season and the epithelium of the vas deferens has been reduced in height giving this duct a transparent appearance in strong light. During this season

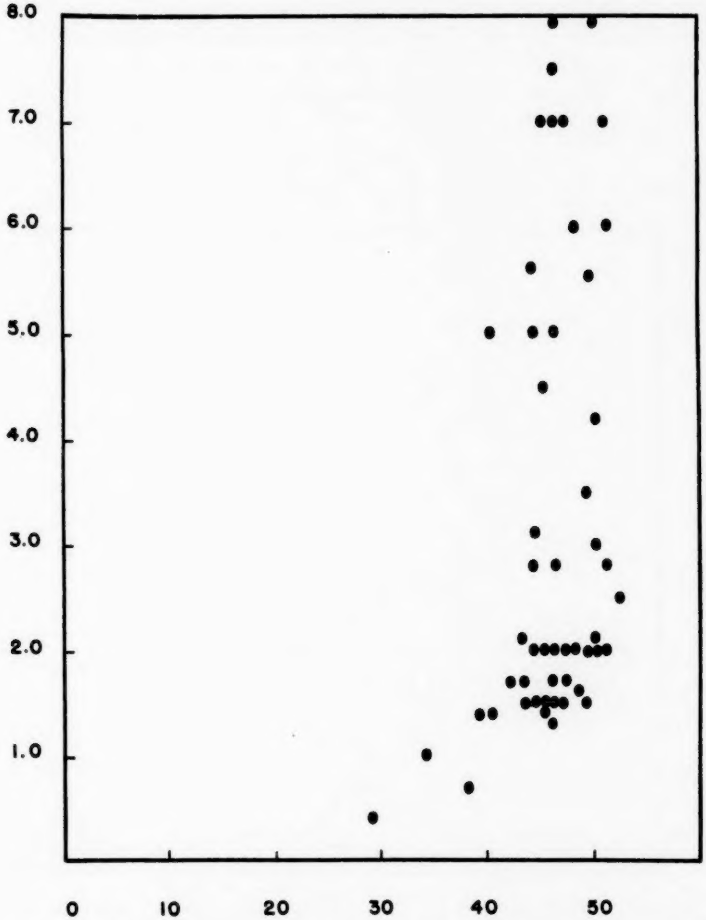

Fig. 6.—Size of largest follicles in ovary of *Uta stansburiana* in February to March. Abscissa: body length in mm; ordinate: size of follicles in millimeters.

mature and subadult males are not distinctively different. Many of the males have very small testes and are obviously immature, but others have testes between 2.0 and 3.0 mm in greatest length, a size to which the testes of adult males may have regressed by this time. Macroscopic examinations of the vasa deferentia are likewise uninformative. Figure 5 does show a separation of males into two fairly distinct groups at this time, but I am not certain that all those in the larger group are adults, although it does seem likely that those in the smaller group are young of the year.

Transitional and Spring Gonads (January to March; Figs. 6 and 7)

The conditions described in the winter ovary are carried into February. The first clear changes in the gonads occur in February or March (see section on reproductive potential) depending upon weather conditions. During this period almost every ovarian follicle that has reached a size of 1.6 mm or greater will show signs of yolk deposition. The follicle first appears cream-colored and more opaque,

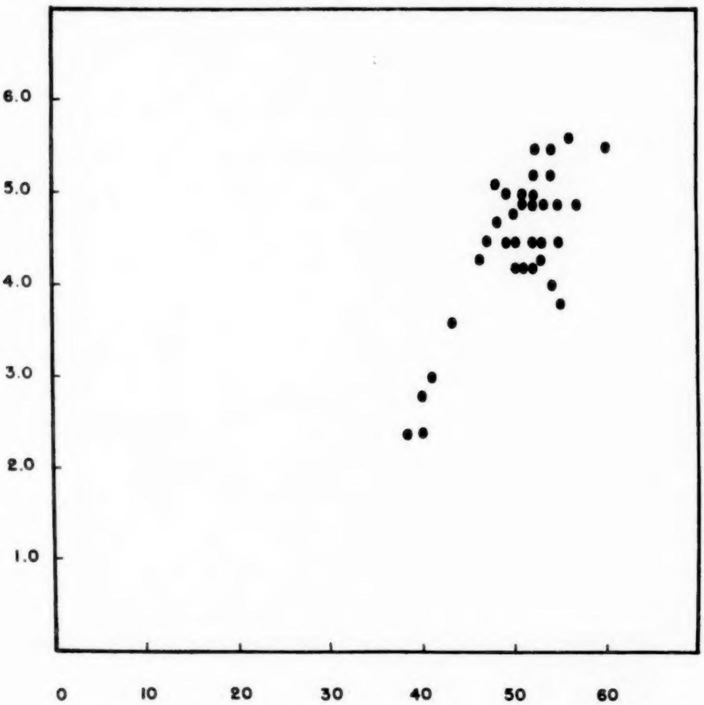

Fig. 7.—Maximum length of testis of *Uta stansburiana* in February to March. Abscissa: body length in mm; ordinate: size of testis in millimeters.

but by the time it has enlarged to 2.0 mm it will appear yellow due to increased yolk content. The yolked follicles are soon clearly distinct from others and accurate estimates of clutch size can now be made by counting them. The largest follicle seen in any population in February was 2.8 mm. In March the yolked follicles increase rapidly in size to a maximum of 8 mm. As most of the largest follicles seen in the ovary are nearer 7 mm, it is assumed that ovulation occurs at this size. This is the same size at which ovulation occurs in *Xantusia*

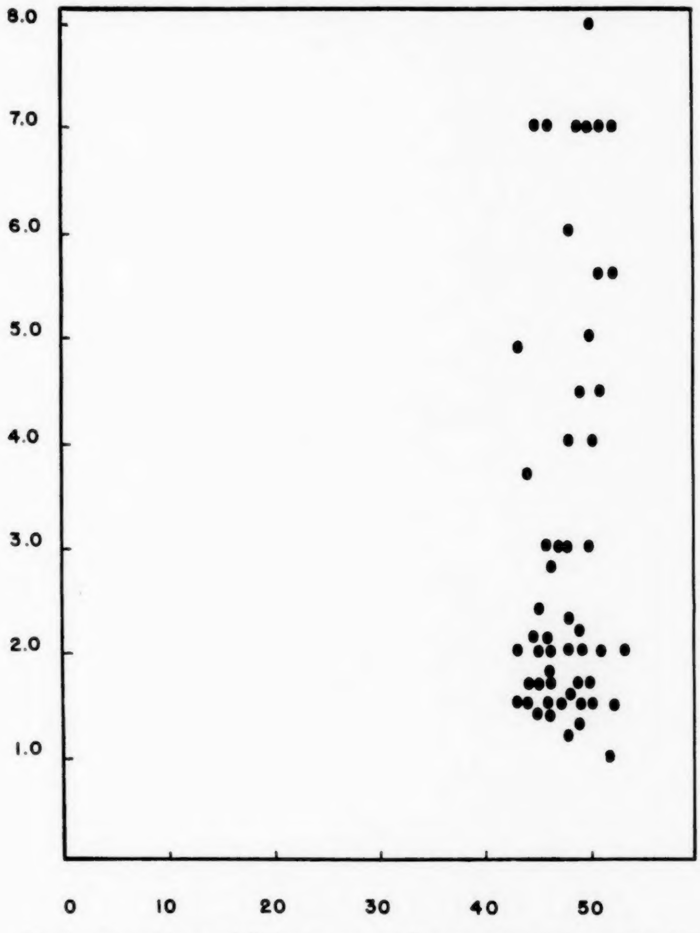

Fig. 8.—Size of largest follicles in ovary of *Uta stansburiana* in April to May. Abscissa: body length in mm; ordinate: size of follicles in millimeters.

vigilis (Miller, 1948), and in *Sceloporus graciosus* (Woodbury and Woodbury, 1945) but this is by no means constant as ovulation may occur at a larger size (10 mm) as in *Amphibolorus muricatus* (Weekes, 1934) or a smaller one (5 mm) as in *Scincella* (= *Lygosoma*) *laterale* (Johnson, 1953).

The first oviducal eggs were noted in the sample of March 8, 1959, in Ward and Winkler counties, but not until April 3 in Armstrong County. However, some females in Armstrong County might have ovulated previous to April 3 as no samples are available from March 13 until April 3. No yolked follicles were present in females of the March 13 sample from Palo Duro which would indicate that ovulation would be primarily in April. In 1960, no ovulation had occurred in females of the two southern populations as late as April 1, but had occurred when the next sample was taken on April 16. Thus, first ovulation was a month later in 1960 than in 1959. By March 27, 1960, only three females examined from Armstrong County

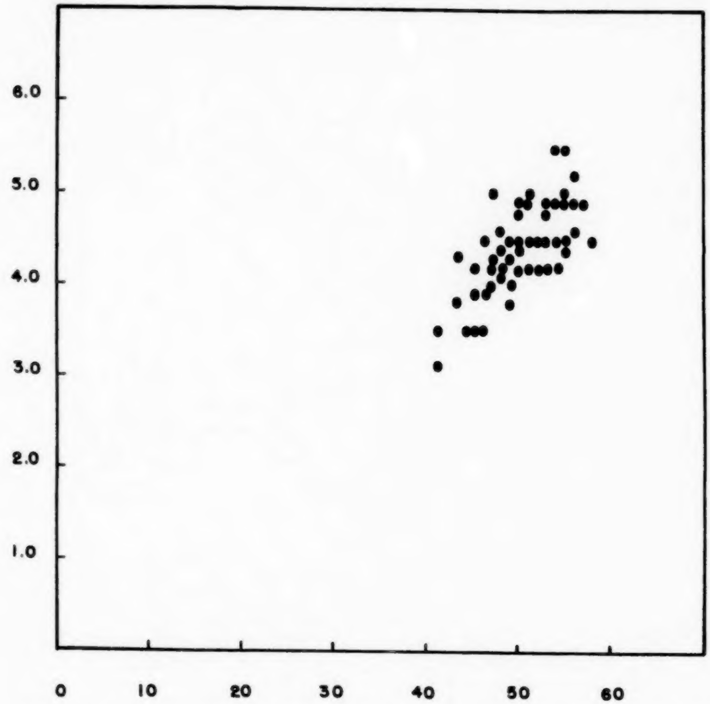

Fig. 9.—Maximum length of testis of *Uta stansburiana* in April to May. Abscissa: body length in mm; ordinate: size of testis in millimeters.

showed any sign of yolk development. Two of these had largest follicles of 2.0 mm and the third, 4.0 mm. It is doubtful that ovulation in 1960 could have occurred prior to mid-April or later. A large sample from this population on April 25 contained several females containing oviducal eggs.

In males the testes and vasa deferentia begin enlargement during this period and become sexually potent. At this time the testes have a compact appearance rather than the flatness often characteristic of winter testes. The vas deferens is tortuously convoluted and expanded by increase in size of the epithelial lining. As can be seen from Figure 7, the testes of almost every male are between 4.0 and 6.0 mm in greatest length. The only smaller ones belong to lizards hatched late the previous summer that have not yet reached mature size.

Reproductive Gonads (April-June; Figs. 8-9)

Most reproduction in these lizards occurs during this period. The testes get no larger than in the previous period, but the tubules of the testes become large and are easily seen through the enveloping tissues.

The ovary goes through a series of cycles like that described in the previous period. After the first and second ovulations, the development of another set of follicles toward ovulation begins. In no instance was a smaller set of follicles beginning yolk deposition prior to ovulation of the previously enlarged ones. This seems to be typical of most lizards, but not of all. Weekes (1934) reports that ovarian follicles in *Amphibolurus muricatus* reach one-half ovulatory size before the first eggs ovulated are laid. It is rare for *Uta stansburiana* to show any follicle enlargement or yolk deposition as long as oviducal eggs are present. The largest follicle seen in a female with eggs was 2.2 mm, but in almost all individuals the maximum is 1.5 mm with no trace of yolk deposition. That yolk deposition and enlargement proceed immediately after oviposition is clear from the observation that females with distinct corpora lutea indicating recent ovulation usually have some follicles developing yolk even though they are always less than 2.0 mm.

The Late Reproductive and Postreproductive Gonad
(July-September; Figs. 10-11)

During this period the vasa deferentia of the male again became more translucent due to regression of the lining epithelium and the testes lose their rounded appearance and become smaller. Few testes exceed 3.0 mm during this period. It is likely, as noted earlier, that most of these individuals are young of the year, but doubtless there are some old adults in the group in which the testes have receded. It is clear from the figure that there are not two distinct groups of lizards with regard to size at this time.

In 1959, most egg laying ceased in July in all three populations.

Only two gravid females were seen in August, one in Armstrong County, the other in the southern populations. It is doubtless these late laying females that produce the young which appear as very small individuals in samples made early the next year (Figs. 1-3). In 1960, only one gravid female was seen in August, this in the southern populations.

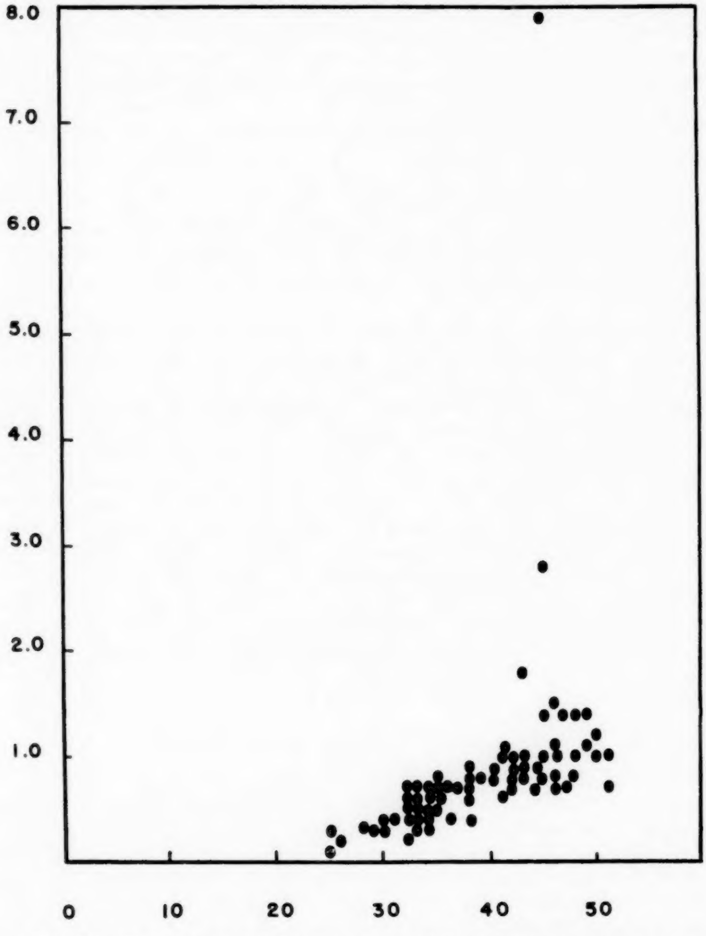

Fig. 10.—Size of largest follicles in ovary of *Uta stansburiana* in August to September. Abscissa: body length in mm; ordinate: size of follicles in millimeters.

Juvenile Gonads

Juvenile lizards appear in the populations primarily in July and later, although occasional individuals hatch in June. The sexes at hatching can generally be distinguished because follicles can be seen in the female gonad. Even when the ovary has not differentiated, the oviduct can be seen as a thin, unconvoluted and almost transparent ribbon extending from the cloaca anteriorly and laterally against the dorsal peritoneum.

The increase in size of the gonads is correlated with an increase in body length as can be seen from Figure 12 in which body length is plotted against maximum follicle size or maximum testis length for juveniles between 20 and 40 mm body length.

During the summer and fall following birth the gonads develop to such an extent that it is frequently difficult to distinguish a mature from an immature individual on the basis of testis or follicle size alone. The vasa deferentia and oviducts are of little additional help because of enlargement of the former and convolution of the latter which obviously occurs well in advance of ovulation. The size of follicles may be as little as 0.1 mm, but most are 0.3 mm and greater and most are less than 1.0 (Fig. 12). It is possible that those females with follicles greater in size than 1.0 mm are old adults.

The Corpus Luteum

The corpus luteum is not often discussed by authors writing on reproduction in lizards, so little information on these structures is

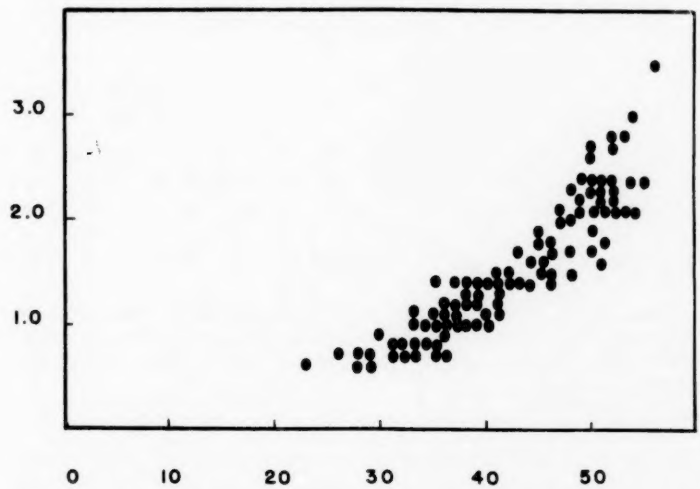

Fig. 11.—Maximum length of testis of *Uta stansburiana* in August to September. Abscissa: body length in mm; ordinate: size of testis in millimeters.

available for most species although some detailed histological studies have been made by several authors including Panigel (1956), Weekes (1934), and Miller (1948). The stages of luteal formation and degeneration described by Weekes (supra cit.) are similar to those observed macroscopically in *Uta stansburiana.*

The corpus luteum in *Uta stansburiana* is a large doughnut-shaped structure which rapidly regresses following ovulation. It does remain distinct throughout preovipositional development of the oviducal egg as shown by the fact that in only 5 females with oviducal eggs was I unable to find lutea; these scars were present in 39 females after egg laying had occurred.

Follicular Atresia

Follicular atresia is discussed later in relation to its influence on reproductive potential, but seasonal data are appropriate here. It was anticipated that the greatest atresia would occur in late summer because at that time some follicles begin enlargement but are not ovulated because of changes in whatever factors (day length?) govern reproduction. The total number of atretics for each month from the beginning of follicle enlargement to the end of the reproductive season are shown below:

Month	*Number of atretics*	*Per cent of total*
February	3	5
March	1	2
April	7	12
May	17	28
June	10	17
July	8	13
August	14	23
Totals	60	100

The tabular data do not show that atresia is most pronounced in late summer, but the August data do not include 8 females which were noted as having atretic follicles, but in which no counts were made. If each of these had only a single atretic follicle, the August percentage would be higher than that of any other month, but not significantly so.

In large atretic follicles the yolk has a peculiarly granular or flocculent appearance rather than the homogeneous appearance of normal follicles. As the atretic follicle undergoes degeneration it becomes a tiny orange to yellow spot.

Interuterine Migration of Ova

After ovulation, the mature egg passes generally to the oviduct on the same side as the ovary from which it originated. Both Legler (1958) and Tinkle (1959) have commented upon the seemingly high percentage of ovular migration in various reptiles from one ovary to

the contralateral oviduct. Such a transfer is inferred to have occurred when the number of corpora lutea and oviducal eggs on one side or the other are not the same.

Of 135 female *Uta stansburiana* in which accurate counts of both eggs and lutea could be made, interuterine migration occurred in 27 (20%). This compares with a figure of 57 per cent occurrence of migration in the box turtle *Terrapene ornata* (Legler, op. cit.).

This ovular migration was from right side to left in 11 and from left to right in 16. In all but one instance, only one egg was involved. In the lone instance of two eggs, two went to each oviduct, but all four came from the same ovary.

It is possible that ovular migration is actually more frequent for it would not be detected if there was a reciprocal exchange of eggs.

Reproductive Potential

Reproductive potential may be determined on three bases. The two most accurate are counts of the number of corpora lutea or of the number of oviducal eggs. Only rarely is there a difference between the number of corpora lutea and the number of eggs present. Always in such cases there were more lutea than eggs indicating that one or more of a given clutch had already been laid. It is not likely that the excess number of lutea represented some resulting from earlier ovulations because these lutea undergo rapid degeneration after egg deposition (see section on corpus luteum). If there were more lutea than eggs, the count of the former was considered the accurate one. Only

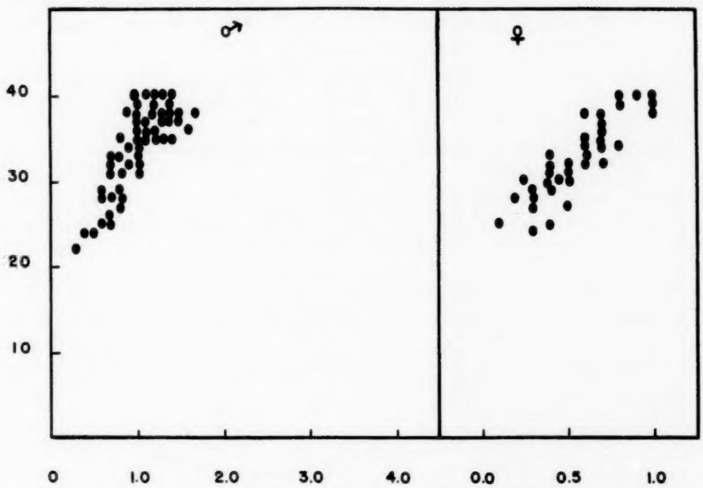

Fig. 12.—Maximum size of testis and of largest ovarian follicles in juvenile *Uta stansburiana* of different sizes. Abscissa: size of testes or of follicles in millimeters; ordinate: body length in mm.

females that were undamaged in capture were used in this part of the study. Follicles and eggs are easily broken in capturing female lizards, making accurate counts difficult or impossible. In some females in which yolk deposition has just begun, it is sometimes difficult to decide which ones will be ovulated and which will not. Therefore, these doubtful individuals were excluded from consideration.

Reproductive potential could be accurately estimated in 363 females containing 1436 eggs, lutea or clearly enlarged follicles, an average of 4.0 per female per clutch. However, as enlarged follicles may not all be ovulated, a comparison was made of potential calculated on the basis of eggs or lutea with that obtained from egg counts. On the basis of enlarged follicles in 194 females, the mean clutch size is 4.2; or the basis of eggs or lutea in 169 females it is 3.9. Most of this difference is attributable to follicular atresia. Follicular atresia is uncommon in *Uta stansburiana* as it was observed in 20 lizards from Winkler County, 21 from Ward County and 7 from Armstrong County, constituting less than 1 per cent of the total number of adults examined. Only 60 atretic follicles were observed in these lizards; in addition, eight females contained an uncounted number, so that the probable total number of atretics seen was about 70 to 75. Thus, possibly 8 to 10 per cent of enlarged follicles undergo atresia.

The reproductive potential on the basis of enlarged follicles was 4.2, on the basis of eggs or lutea it was 3.9. This is a difference of just over 7 per cent. Therefore the decrease can be attributed entirely to atresia. At any rate, both figures (i.e., 4.2 and 3.9) when rounded show an average clutch size of four. Counts of enlarged follicles are accurate for estimates of clutch size. Fitch (1954) in a study of the lizard *Eumeces fasciatus* remarks that counts of enlarged follicles in that species are high compared with counts of oviducal eggs. However, no figures are given in support. He maintains that there are usually small ova of intermediate size between the large ovulatory ones, and the small white ones without yolk. This situation does not exist in *Uta stansburiana* unless counts are attempted during the nonreproductive season before yolk deposition. He also mentions that among the large follicles there may be some that are much smaller than others and which might not become part of the same clutch. This situation does occur in *Uta stansburiana* and occasionally it is difficult to determine objectively which will be ovulated, but this is rarely true.

Reproductive potential in most lizards and in most reptiles varies directly with the size of the female. The lizards were divided into four arbitrary size groups and the mean potential for a female in each group calculated as follows:

Size class (in body length)	Number of females	Mean potential
35-39	4	3.3
40-44	89	3.6
45-49	230	4.0
50-54	40	4.9

It is evident that there is an increase with increase in size with the biggest increase coming in lizards over 50 mm in length.

The mean reproductive potential is only slightly different in the three populations studied. The potential in the northern population is 4.2; in the Winkler County population, 4.2; and in Ward County, 3.6. That this difference is not due entirely to differences in the percentages of size groups in the three populations may be seen from the following tabulation.

Sample area	*Size classes and per cent of females in each*			
	35-39	*40-44*	*45-49*	*50-54*
Armstrong	3%	39%	55%	3%
Potential	3.3	3.7	4.0	5.7
Winkler	0%	10%	69%	21%
Potential		3.7	4.1	4.8
Ward	1%	31%	64%	5%
Potential	3.0	3.3	3.7	4.6

There do not appear to be any differences in the Armstrong and Winkler County populations despite the difference in size group frequencies except in the size group 50-54 in which the potential of Armstrong County females is almost one egg greater. However, this difference may be one of sampling bias because only a few females of this size are available from Armstrong County (see Fig. 3). The differences between Armstrong County and Ward County are small, but may be important because the potential is greater for every size group in Armstrong County than Ward. It may be that there are selective pressures peculiar to the Ward County population favoring a smaller clutch size. This would not be possible as Lack (1954) has pointed out unless lizards hatching from smaller clutches have a survival advantage over those hatched from larger clutches. That such differences in clutch size may occur in lizards subjected to different competitive situations and that clutch size may be inherited has been demonstrated in a study of the lizard *Lacerta sicula* by Kramer (1946).

The possibility of year to year variation in reproductive potential was also studied. The samples of 1959 were compared with those of 1960. It was unfortunately necessary to omit the Armstrong County data because, although covering a longer period of time, there were not sufficient large samples. The mean potential of Ward County females in 1959 was 3.7, in 1960, 3.5. Comparable figures for Winkler County are 4.6 and 3.9, respectively. Although other explanations for the big change in the Winkler population are possible, the most plausible is a change in frequency of the size classes. The data for 1959 and 1960 do show a decrease in percentages of individuals in the larger size groups as shown below:

		35-44	*45-54*
Ward County	1959	27%	73%
	1960	34%	66%
Winkler County	1959	47%	96%
	1960	15%	85%

The larger decrease is 11 per cent in Winkler County, but this is not much greater than the 7 per cent decrease in Ward County, so the decrease in potential in Ward County may be completely attributable to this change in percentage, but other factors may be involved in the more significant reduction occurring in Winkler County.

The clutch size may also vary with reproductive season. The average clutch size for the entire reproductive season falls but little from March to June, but does decrease rapidly in July and August. This decrease is doubtless due in part by the last of several clutches in a female containing fewer eggs, but is also due to the fact that some of these late clutches are by females (young of the previous summer) that matured late in the current reproductive season and are producing their first clutch. Although I have not made measurements, it is my impression that the eggs in the small clutches of only two eggs are distinctly larger with more yolk than eggs from larger clutches.

The mean figures for clutch size based on large samples from all populations combined are as follows: March, 4.2; April, 4.2; May, 3.9; June, 3.9; July, 3.1; August, 2.7. These figures indicate that the last clutch of the season is about one egg smaller than the first

Much of the data in the literature on reproductive potentials of lizards is difficult to compare because usually the number of females examined is small; they frequently come from different parts of the range, are of different sizes and collected at different seasons. The data available on North American species are shown in Table III.

These data show that smaller species generally have smaller clutches and that viviparous forms have fewer embryos than oviparous species in the same genus that are of about the same size. Most of these authors note an increasing clutch size with an increase in body size of the female. Exceptions to this are *Sceloporus merriami* (Chaney and Gordon, 1954) and *Scincella laterale* (Johnson, 1953) in which there seems to be no correlation between body size and clutch size.

Fitch (1956) in a study of the collared lizard (*Crotaphytus collaris*) states (p. 237): "Except for anoles which produce only one egg at a time, iguanids have not been known to produce more than one clutch per season." Fitch reported that one collared lizard observed by him laid two. Some iguanid lizards as shown in Table III certainly lay more than one as does *Uta stansburiana* reported in this paper. The data of Chaney and Gordon (1954) on *Sceloporus merriami* do indicate more than a single clutch in that species, too. It seems more likely that multiple clutches will prove to be typical in iguanid species except in viviparous forms with long periods of intrauterine egg development.

Number of Clutches per Season

It was obvious from this study that females lay more than a single clutch per year because many of them have distinct corpora lutea and

yet have follicles in the process of yolk deposition and enlargement. Unfortunately corpora lutea do not persist for any length of time after egg deposition, and no observations could be made on frequency of laying by individual females, so the probable number of clutches per year must be calculated indirectly.

The length of time from which a majority of females have first begun yolk deposition in the spring (February-March) to the time at which a majority contain oviducal eggs will give a measure of the time required for the development of one clutch. This figure can then be divided into the length of the reproductive season defined as the time from which most individuals show follicle enlargement to the

TABLE III.—Comparison of mean reproductive potential per clutch for 18 North American lizards reported in the literature (the V after name of a species indicates it is viviparous)

Species	Author	Average clutch size	Number of clutches counted	Maximum no. of clutches per season
Cnemidophorus sexlineatus	Fitch(1958)	3.0	112	2
Gerrhonotus m. multicarinatus	Fitch(1935)	11.6	13	—
Gerrhonotus m. webii	Fitch(1935)	12.4	7	—
Gerrhonotus coeruleus shastensis (V)	Fitch(1935)	6.3	15	—
Xantusia vigilis (V)	Miller(1951)	1.8	78	1
Eumeces fasciatus	Cagle(1940)	9.2	25	—
Eumeces fasciatus	Fitch(1954)	9.1	182	—
Eumeces obsoletus	Fitch(1955)	11.4	13	—
Eumeces septentrionalis	Breckenridge (1943)	8.8	19	—
Scincella laterale	Johnson(1953)	3.3	31	2
Anolis carolinensis	Gordon(1956)	1.0	—	6-9
Dipsosaurus dorsalis	Norris(1953)	3-8	—	—
Holbrookia texana	Cagle(1950)	6.6 June-July	14	Several
		3-6 August	10	—
Crotaphytus collaris	Fitch(1956)	7.6	29	2
Sceloporus merriami	Chaney and Gordon(1954)	3.7	27	1?
Sceloporus undulatus	Crenshaw(1955)	7.6	11	Possibly more than 1
Sceloporus olivaceus	Blair(1960)	11.3 yearlings 18.4 2-year 24.5 3-year	—	4 except yearlings
Sceloporus cyanogenys (V)	Hunsaker(1959)	12.6	7	—

time at which most individuals have ceased laying. The data presented are for Ward and Winkler county populations only.

In 1959, the majority of females had follicles just beginning enlargement on February 13, while in 1960 the majority had not begun enlargement until March 10. In 1959, most females had oviducal eggs on March 22; in 1960, on April 16. Thus, the time for the development of the first clutch was 38 days in 1959, 37 in 1960.

The length of the reproductive season was 141 days in 1959 and 121 days in 1960. Dividing these figures, respectively, by 3.8 and 3.7 gives 3.7 and 3.3 for the number of clutches.

It may be argued that the development of the clutches after the first will proceed more rapidly because of higher temperatures and a longer activity period. However, I think that any one female laying more than 3 clutches is unlikely because the figures obtained allow no time for oviducal retention of the eggs which must be at least one week, but probably longer. Too, the reproductive season for any single female will probably not be as long as the figure above because females maturing late in their second season will reproduce late and thus extend the reproductive season of the population beyond what it would be for an individual.

By multiplying an average figure of three clutches per year by the mean potential for each female, an average annual potential per female for each population would be as follows: Ward, 10.8; Winkler, 12.6; Palo Duro, 12.6 if three clutches per year is also normal there, but data are insufficient to be certain of this.

On the same basis, the proportion of the potential contributed by each size class can be calculated as shown below:

Size classes (mm)	Armstrong County	Winkler County	Ward County
35-39	9.9	—	9.0
40-44	11.1	11.1	9.9
45-49	12.0	12.3	11.1
50-54	17.1	14.4	13.8

By having the percentage of females of each size class in a given population at the beginning of the reproductive season would make possible the calculation of the number of eggs laid in a given population. Such an estimation was attempted in the summer of 1960 in the Winkler population in a 10,000 square yard area. All females in the population were marked. Of the total number of adults marked 18 had their home ranges, based on at least 3 captures, largely confined to the study area or immediate margin. The size distribution of these females is as follows and the potential number of eggs is:

40-44 mm	1	11
45-49 mm	14	172
50-54 mm	3	43
	Total	226

The total number of hatchlings potentially produced was 226. The total number of hatchlings marked in the same area was 174. The juveniles have exceptionally strong homing tendencies, so little emigration or immigration occurred making the above figures more reliable. Although 174 young were marked in the area, unmarked young still were present on the last trip in late October showing that the actual number was greater than 174.

Relation of Potential to Total Number of Ovarian Follicles

Counts were made in some females of all macroscopically visible follicles to determine if such counts, for example during the winter, were useful in estimating reproductive potential for the following year. Counts were also made in juveniles and in adults at all seasons. It was also hoped that counts of total numbers might indicate number of clutches deposited. The data are shown in Table IV.

The total number of ovarian follicles at any season will not give an accurate estimate of reproductive potential. The average number of follicles present in adult females during the winter is about the same as in prereproductive females during January to March and both these counts are about the same as the counts made just prior to first ovulation, so these three groups could be combined for comparative purposes. It can be seen that there is a slight decrease in the mean of all size groups between that just prior to ovulation with that just afterward. The average decrease for all size groups is from

TABLE IV.—Total number of follicles in female *Uta stansburiana* of different size groups at different seasons and during different stages of the reproductive cycle (all figures shown are means except those in parentheses which are number of specimens)

Period	35-39 mm	40-44 mm	45-49 mm	50-54 mm
Jan., Feb., March (Prereproductive)	17.0(5)	17.4(26)	17.5(26)	17.5(2)
	Mean of all groups *17.4*			
July, Aug., Sept. (Post reproductive)	—	15.0(2)	16.1(12)	—
	Mean of all groups *15.9*			
October-December (winter)	15.0(1)	15.6(8)	18.0(7)	18.0(2)
	Mean of all groups *16.8*			
Just prior to ovulation	16.0(1)	18.3(12)	18.3(30)	22.8(6)
	Mean of all groups *18.8*			
After ovulation while oviducal eggs still present	13.0(1)	16.4(8)	16.5(47)	18.0(1)
	Mean of all groups *16.5*			
After egg deposition, but prior to new follicle enlargement	—	20.7(7)	19.2(22)	—
	Mean of all groups *19.6*			

18.8 to 16.5, a drop of 2.3. If it were assumed that no new follicles appeared just after ovulation this figure of 2.3 could be used as one measure of average clutch size. However, counts of corpora lutea and eggs were also made in those females in which total number of follicles was counted. The actual average clutch size of these females was 3.8.

Ovulation seems to stimulate follicle development. The average number of follicles is greater after ovulation and subsequent egg deposition than at any other time.

The average number of follicles in young lizards was 12.7. From this low, the mean number tends to increase with an increase in body size as can be seen in Table IV. Other than follicles with yolk, no other size group will give an accurate estimate of potential nor are counts of total number of follicles suitable for that purpose.

Conclusions

Populations of *Uta stansburiana* within 300 miles of one another and belonging to the same subspecies (*stejnegeri*) may differ from one another in several biological attributes.

The sex ratio is little different from 50:50 in any of the three populations regardless of age group or season.

The ratio of juveniles to adults is different from one population to another at different seasons, but data indicate that in all populations over 90 per cent of the individuals are mature during the reproductive season at an age of one year or less.

There is an annual turnover of most of each population. This fact cannot be established satisfactorily from mass samples, but could be from study of marked animals in a study population.

Females reach maturity at a smaller size than males and generally do not grow to the large size of the males. Size at maturity varies between the three populations. The smallest mature individual was 38 mm, the largest individual recorded, 60 mm.

A comparison of age at maturity of North American lizards indicates the iguanid lizards mature faster than scincids regardless of size of the species. Age at maturity may vary geographically.

The maximum size of ovarian follicles in a nonreproductive female is 1.7 mm. These begin enlargement and yolk deposition in February and March and approximately 38 days are required before these follicles will be ovulated at a size of 7 to 8 mm. The initiation of ovarian development in the spring is greatly affected by weather conditions prevailing at this time.

Testis enlargement takes place simultaneously with follicle enlargement until June and July when the testes and vasa deferentia undergo regression.

Oviducal eggs first appear in March and April and for the last time in August.

After ovulation, the corpus luteum formed generally remains distinct until after egg deposition. As long as oviducal eggs are present no ovarian follicles begin enlargement or yolk deposition, but this

process does begin after deposition and sometimes when corpora lutea are still evident.

The gonads of juvenile lizards are very small at birth, but follicles and oviduct are usually differentiated even then, so the sexes are usually easily distinguished. The increase in size of follicles and of the testis is correlated directly with increased body length.

During development of yolked follicles some of these will undergo atresia, but this is uncommon and does not exceed 10 per cent in all adult females examined.

Following ovulation, one egg (in one case two) may be transferred from the ovary to the contralateral oviduct. This occurred in 20 per cent of the females examined. Comparative percentages in other reptiles are presented.

Reproductive potential can be calculated accurately on the basis of the number of enlarged yolked follicles, the number of corpora lutea, or the number of oviducal eggs. Little difference exists in estimates on any of these bases. Counts or measurements of follicles in nonreproductive females cannot be used for estimating potential.

Reproductive potential is lower in smaller lizards, lower late in the season, and in one population compared with the other. Year to year variations are also evident and generally correlated with the percentages of each size group of lizards in the population.

A comparison of reproductive potential in North American lizards shows that it is lower in viviparous forms, in smaller species, and in scincid as opposed to iguanid lizards.

Uta stansburiana probably lays three clutches of eggs per year. Multiple clutches seem to be characteristic of many North American lizards.

A study of the total reproductive potential of a lizard population was made by knowing the number of females present in a study area and their sizes. The figure for their potential egg production (226) was very close to the actual number of hatchlings marked in the study area (174).

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Variation in Populations of Brown Snakes, Genus Storeria, Bordering the Gulf of Mexico

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Abstract: Examination of specimens of *Storeria* from coastal areas of Louisiana and Texas indicates the existence of a distinctive population inhabiting the coastal marshes. On the basis of color pattern and scutellation this population is sharply distinct from populations of *Storeria dekayi* on adjacent higher ground and appears closely allied to *Storeria* of Mexico, Guatemala and Honduras. The few specimens suggesting possible interbreeding with contiguous high ground populations come from areas of ecological disturbance and appear to represent occasional hybridization, rather than an indication of intergradation.

Specimens believed by Trapido to represent intergrades between *Storeria dekayi temporalineata* and *S. d. texana* or *S. d. wrightorum* were derived from the distinctive marsh population, and the southern and northern groups of subspecies placed by Trapido in the species *Storeria dekayi* thus appear to be reproductively isolated. *Storeria tropica* Cope is therefore revived for the southern group, with four subspecies; *Storeria tropica tropica, Storeria tropica anomala, Storeria tropica temporalineata,* and *Storeria tropica limnetes,* subsp. nova, the population of the Louisiana and Texas coastal marshes.

In his monograph of the snakes of the genus *Storeria,* Trapido (1944) recognized six subspecies of *Storeria dekayi,* distributed from the northeastern United States to Guatemala and Honduras. Three of these subspecies, *S. d. texana, S. d. wrightorum,* and *S. d. dekayi* occur north of the Rio Grande and replace each other from west to east, between the Great Plains and the Atlantic Coast. As defined by Trapido, the easternmost subspecies, *dekayi,* is found from the Atlantic Seaboard to the western side of the Appalachians. Its northern limit is the limit of the species distribution in Quebec and it intergrades with *S. d. wrightorum* over a broad area extending from the Carolinas around the southern Appalachians and northward to Illinois. Subspecies *wrightorum* extends from this zone of intergradation westward across the Mississippi valley and intergrades with *S. d. texana* along a line from Iowa to western Louisiana. Subspecies *texana* is found between this line and the eastern edge of the Great Plains and extends southward to the gulf coast of Texas and into Mexico as far south as Hidalgo.

The three remaining subspecies which Trapido recognized are found in Mexico, Guatemala and Honduras. They are described as replacing each other southward along the gulf coastal plain, with *S. d. temporalineata* extending from the Rio Grande south into Veracruz, where *S. d. anomala* occurs. The latter is said to be characteristic of an area about the towns of Orizaba and Jalapa. It presumably intergrades with *S. d. tropica,* which inhabits the Atlantic drainages of Guatemala and Honduras.

The three southern subspecies were based on a small number of specimens and their relationships and distributions are not clearly established in Trapido's monograph. In the northern group, where material was much more abundant, the three subspecies are represented as intergrading over relatively broad strips along their mutual boundaries (*S. d. dekayi* x *S. d. wrightorum* and *S. d. wrightorum* x *S. d. texana*). In contrast to these broad zones of intergradation Trapido indicated, without comment, a very peculiar pattern of intergradation between the southern group, represented here by *S. d. temporalineata,* and the northern group represented by *texana* and *wrightorum*. Subspecies *temporalineata,* as was indicated above, was said to reach the northernmost limit of its range at the Rio Grande. In his discussion of this subspecies, however, Trapido noted that specimens showing its characteristics had been collected as far to the northeast as Mississippi. He designated these specimens, some 20 in number, as intergrades between *temporalineata* and one or the other of the two northern subspecies occurring in this region. With one exception, a specimen from Natchitoches Parish, Louisiana,[1] the supposed intergrades were restricted to a narrow strip immediately adjacent to the coast, implying an area of intergradation some 700 miles long, and generally less than 20 miles wide. Such a column-like intergradation pattern would seem to require an explanation. In the words of Schmidt (1953) it is, "not geographically intelligible."

The localities from which the presumed intergrades were taken, with the aforementioned exception, are in or at the edge of the great coastal marshes of Louisiana and east Texas. Trapido's data thus suggest that a distinctive marsh population exists in this area, rather than a tenuous and peculiarly penetrating kind of intergradation. In 1949 the growth of the Tulane University Collections had led to the accumulation of a sufficient number of specimens of *Storeria* from the Louisiana marshes to confirm the existence of such a population and to make an analysis of its relationships possible. Studies upon which this report is based were begun at that time at the suggestion of Dr. Fred R. Cagle of Tulane and have been pursued intermittently since. The author wishes to express his gratitude to Dr. Cagle for encouragement in the initial phases of the study and to Mrs. Emily Reid, staff artist of the Department of Zoology, University of California, Berkeley, for final preparation of the figures.

MATERIALS AND METHODS

One hundred and eighty-seven *Storeria* from Mississippi, Louisiana, and Texas; the Mexican states of San Luis Potosi, Nuevo

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[1] This specimen, CU7364, from Chastine, La. is in poor condition with markings somewhat obscured, but appears to be typical of *S. d. wrightorum* in all features. The locality listed by Trapido, Creston, is apparently an error.

Leon, Veracruz and Puebla; Guatemala and Honduras, have been examined.

The author is indebted to the following institutions and individuals for opportunity to examine specimens. The abbreviations to be used subsequently are shown in parentheses: Dr. Fred R. Cagle, Tulane University (TU); Dr. Richard G. Zweifel, American Museum of Natural History (AMNH); Dr. Arthur Loveridge, Museum of Comparative Zoology, Harvard University (MCZ); Dr. Doris M. Cochran, United States National Museum (USNM); the late Karl P. Schmidt, Chicago Natural History Museum (CNHM); Dr. Norman Hartweg, University of Michigan Museum of Zoology (UMMZ); Dr. William J. Hamilton, Jr., Cornell University (CU); Dr. E. Raymond Hall, Museum of Natural History, University of Kansas (KU); Dr. Bryce C. Brown, Baylor University (BU or BCB); Dr. Robert C. Stebbins, Museum of Vertebrate Zoology, University of California (MVZ); Mr. Richard E. Etheridge, Department of Zoology, University of Michigan (REE), and Mr. Roger Conant of the Philadelphia Zoological Garden for aid in obtaining material from the collections of the Academy of Natural Sciences of Philadelphia.

Color pattern, body proportions, size, and the number of ventral and subcaudal scales were the basis for analysis of geographic variation. Data recorded for each specimen examined were as follows: sex; snout-vent length; tail length; number of ventral scales, beginning with the first unpaired scale between the chin shields and not including the divided anal; number of subcaudal scales, beginning with the first scale to reach the midline behind the vent and including the conical scale at the tail tip; upper and lower labials. Head markings were recorded on a mimeographed diagram of the head in lateral view. Written descriptions of the markings of the upper and lower labials and the anterior temporal as seen on the left side, or on the right if the left side of the head was damaged, supplemented the diagrams.

PATTERNS OF VARIATION

The populations originally described by Trapido were distinguished primarily on the basis of differences in scutellation and color pattern. In respect to the latter, the six subspecies fall into two distinct groups. The northern group is characterized by the presence of dark markings on the upper labial scales and by the presence of a vertical dark bar across the anterior temporal (*S. d. dekayi* and *S. d. wrightorum*), or by an anterior temporal with only a narrow dorsal edging of dark pigment (*S. d. texana*). The southern group (*S. d. temporalineata, S. d. anomala* and *S. d. tropica*) is characterized by the absence or near absence of labial markings, and by the presence of a fine median horizontal dark line on the anterior temporal scale. Superficial examination may permit confusion between this line and the dark dorsal edging commonly found on this scale in *S. d. texana,* but careful observation shows these two patterns to be distinct.

In counts of ventral and subcaudal scales, numbers are lowest in specimens from the northeast and increase to the southwest in

the northern group of subspecies. In the southern group the counts are characteristically slightly higher, but there is a considerable overlap with the highest of the counts found in *S. d. texana* from Mexico.

In attempting to ascertain the status of the population of the coastal marshes the most critical indication of relationship would appear to lie in color pattern. In respect to the marking of temporal and labial scales referred to above this population falls clearly with the southern group and without exception specimens from the marshes of the Mississippi delta and the coast to the westward conform to the color pattern characteristic of Trapido's Latin American subspecies. The recording of individual head markings on standard diagrams provides a basis for demonstration of the distribution of the different color patterns and the distinctions between them as shown in Figure 1. Composite diagrams representing the aggregate of head markings of all individuals in samples from selected localities are shown. The composite diagrams were prepared from individual records by filling in all the markings shown in each series of specimens on a single tracing-paper overlay. Since this technique sums all the head markings to be found in a sample, it tends to emphasize any similarity which exists between adjacent populations by giving a single intermediate individual as much weight as a large number of identical and divergent ones. Despite this bias the distinctness of the marsh populations from the contiguous populations on higher ground and the affinity of the former to the southern group of subspecies are clearly shown in the figure. Comparison of the mid-temporal line as found in southern and marsh populations may be made with the dorsal dark edging shown in populations of *S. d. texana* represented by diagrams A and B.

Additional points may be made with reference to Figure 1. On the southern Texas coast the marshes disappear but a series of offshore bars does occur. Few specimens are available from this area, but those which have been examined support the conclusion that this strip of arid coast isolates the marsh populations from those of similar color pattern to the south. The coastal islands are apparently inhabited by populations typical of subspecies *texana* (e. g. the specimens from St. Josephs Island represented by diagram "A". These specimens, eleven in number, are a single adult female and her 10 young — UMMZ 72355 A-K). A second point is that Figure 1 suggests a useful diagnostic character overlooked by Trapido. While there is considerable variation in the markings of the temporal scale, and of the upper labials in general, the three northern subspecies are consistent in the presence of dark pigment on the most posterior scales of both the upper and lower labial series, whereas the marsh and southern populations are equally consistent in lacking such a dark marking at the corners of the mouth.

A final point to be made in reference to the figure is that *Storeria dekayi victa* (diagram "E" is taken from Trapido's plate) shares this characteristic (absence of a spot at the corner of the mouth) with the coastal populations which are the subject of the present paper

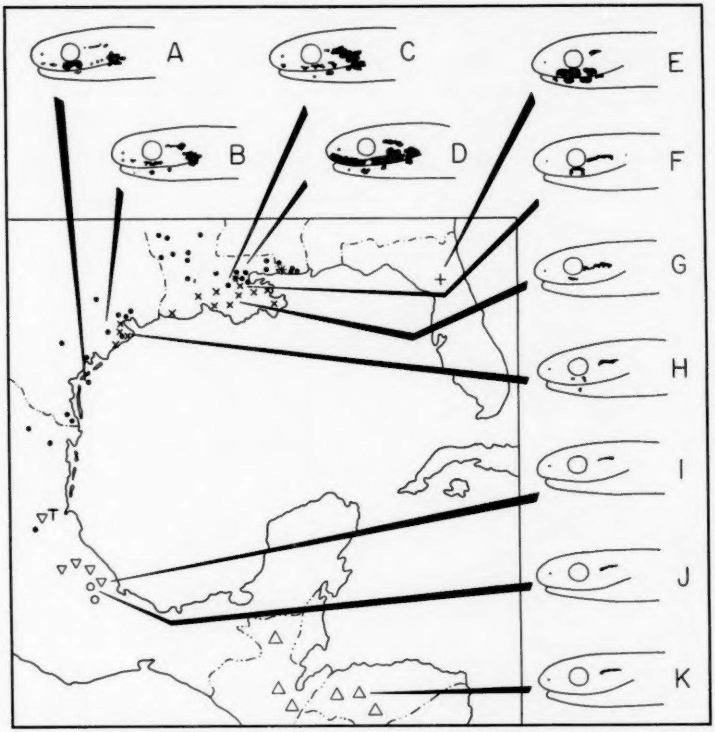

Fig. 1.—Localities from which specimens were examined and head markings in selected populations. Taxonomic assignment of the specimens is indicated as follows: *Storeria dekayi*—solid circles; *Storeria tropica limnetes*—crosses; apparent hybrids between *S. dekayi* and *S. t. limnetes*—asterisks; *Storeria tropica temporalineata*—inverted triangles; *Storeria tropica anomala*—open circles; *Storeria tropica tropica*—erect triangles. The northernmost record for *S. t. temporalineata,* indicated by the superscript[T], is based on Trapido (1944). The specimen was not seen by the present author. The diagrams of head markings are composites of all markings in a particular sample as follows: A—10 specimens from St. Joseph's Island, Texas; B—4 specimens from Harris and Brazoria counties, Texas; C—13 specimens from New Orleans, La.; D—6 specimens from Livingston and St. John the Baptist Parish, La.; E—1 specimen of *Storeria dekayi victa,* Alachua County, Florida, the diagram taken from Trapido's illustration (Trapido, 1944, p. 40); F—4 specimens from Orleans and Jefferson parishes, La.; G—4 specimens from Terrebonne and LaFourch parishes, La.; H—4 specimens from Harris and Brazoria counties, Texas; I—2 specimens of *Storeria tropica temporalineata* from the State of Veracruz, Mexico; J—1 specimen of *Storeria tropica anomala* from the State of Veracruz, Mexico; K—3 specimens of *Storeria tropica tropica* from the Subirana Valley, Honduras.

and this fact should probably be taken into account along with the observations of Neill (1950) in a reconsideration of its relationships.

Further analysis of the color pattern affinities of the marsh population may be carried out by concentrating attention on the total number of upper labials on which any black pigment occurs. The histograms in Figure 2 show that of 53 specimens from the marshes, 50 have 3 or fewer labials with such pigment (94%), while 96 of

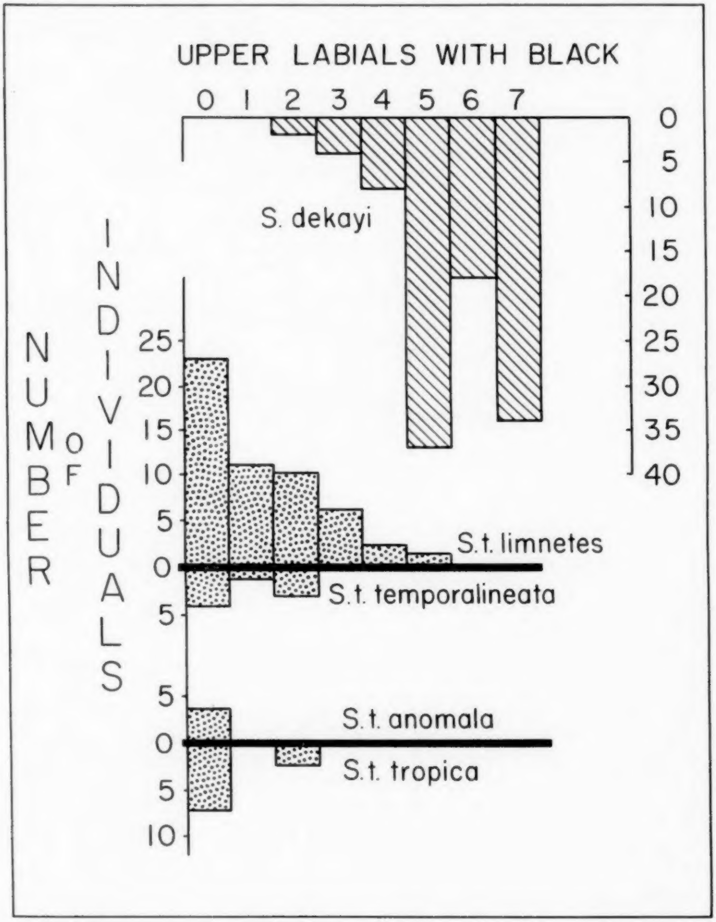

Fig. 2.—Frequency histograms showing the number of upper labials bearing dark markings in the samples of *Storeria dekayi* and *Storeria tropica* examined. Vertical scales indicate the number of individuals.

101 specimens from adjacent higher ground (95%) have 4 or more labials with dark pigment.

An analysis of the body proportions, as indicated by the ratio of total length divided by tail length, showed no significant differences

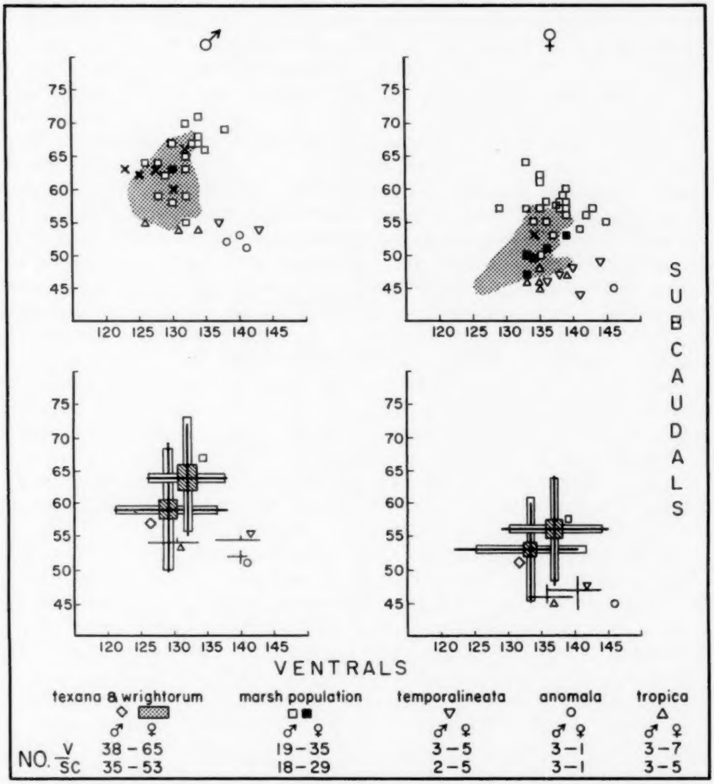

Fig. 3.—Scatter diagrams and modified Dice-Leraas graphs showing counts of ventral and subcaudal scales. The Dice-Leraas graphs show two standard deviations and two standard errors on either side of the means, which are indicated by the junctions of the lines indicating the range. Ranges and means only are indicated for southern populations of *Storeria tropica.* The shaded area, used in the interest of clarity to indicate the scatter of counts for *Storeria dekayi,* shows the area of concentration of scatter points only. Six extreme males and six extreme females of this species fall outside the shaded area. These are included in the Dice-Leraas graphs and in the totals of specimens indicated across the bottom of the figure. Solid squares indicate specimens of *S. t. limnetes* from Cameron Parish, La., and from Texas. Specimens intermediate in color pattern between *S. t. limnetes* and *S. dekayi* are indicated by crosses.

between marsh and high ground populations. With respect to size, comparison of total lengths supports an impression that snakes from the marshes average larger. Total length of 16 adult males and 27 adult females from the marsh population in Louisiana ranged respectively from 215 to 384 mm and 219 to 411 mm with means of 293 and 320 mm. In the high ground populations from Louisiana 22 males varied from 183 to 326 mm with a mean of 261 and 30 females varied from 186 to 405 mm with a mean of 285. Thus, in the Louisiana populations marsh animals average about 12 per cent longer.

Analysis of ventral and subcaudal counts is carried out in Figure 3 using scatter diagrams and modified Dice-Leraas graphs. In the scatter diagrams the marsh specimens, represented by squares, tend to have higher counts of both subcaudal and ventral scales than do specimens from the adjacent populations of *S. d. wrightorum*, *S. d. texana* and their intergrades (stippled area) taken from the adjacent higher ground. Moreover, the marsh populations are not intermediate with respect to subcaudal scales, but instead represent the extreme. Surprisingly the marsh population is most sharply separated from the populations to the south which share the same color pattern. Specimens from Harris and Brazoria Counties, Texas, are represented by the solid squares and show a tendency to be intermediate between those from the marshes to the north and specimens designated as *S. d. temporalineata* from Mexico. The Dice-Leraas graphs indicate that the differences between marsh and high ground populations are statistically significant though not to the extent usually accepted as a basis for taxonomic distinction.

Referring once more to Figure 1 and noting the localities from which the specimens referred to were taken, it is clear that a distinctive form of *Storeria* inhabits the coastal marshes of Louisiana and Texas. The taxonomic status of this population hinges upon its relationships to the southern and northern subspecies groups, and, conversely, the relations of these groups to each other depends upon the status of the marsh population. On the basis of color pattern the *Storeria* of the marshes seems clearly to be a representative of the southern group, while on the basis of scutellation it is distinct from the same southern populations on a level which can best be indicated by subspecific recognition. The critical question is that of intergradation between the marsh population and populations representing the northern group of subspecies.

Sympatry of the marsh and high ground forms has been observed along the Mississippi River levees in and near New Orleans where they may occasionally be taken under the same bit of cover. Specimens characteristic of both forms have also been examined from Jackson Lake, Brazoria County, Texas. Since the marsh population occupies such a narrow strip, the massive zones of intergradation found between the subspecies which comprise the northern group are not possible and it might appear that the very narrowness of the range of the marsh population argues against the existence of

any extensive gene exchange with the high ground populations. However, the Gulf Salt Marsh Snake, *Natrix sipedon clarki,* occupies the same marshes and maintains its identity while interbreeding with freshwater forms (*N. s. confluens* and *N. s. fasciata*) so it should be assumed that selective forces can maintain subspecific differences in the area with which we are concerned.

Since scale counts overlap so broadly, evidence of intergradation must be sought primarily on the basis of intermediacy of color pattern. Three criteria might aid in recognition of possible intergrades: presence of both a temporal line and dark pigment on the 7th upper and lower labials, reduction in size or absence of the dark mark at the corner of the mouth, or a temporal marking intermediate between the horizontal line and the diagonal bar. Scale counts of individuals having such color patterns might be expected to fall in the zone of overlap. Among 164 specimens examined from the marsh population and from the populations of *S. d. texana* and *S. d. wrightorum* peripheral to the marshes, 6 specimens have been found which show some of these features. Two of these (TU 14255 and TU 14256) are intermediate in color pattern but have ventral scale counts below the extreme range of the marsh population (123 and 125, respectively). A third specimen (TU 14265) from the same locality as the two referred to above has the 7th labials unmarked, a high ventral count, and a heavy horizontal dark bar on the dorsal third of the temporal. These specimens come from Hancock Co., Mississippi, at the eastern terminus of the marshes. A specimen from nearby Biloxi, Mississippi, and two from New Orleans (UM 76821, TU 12163, USNM 12923) are similarly intermediate in both scale counts and color pattern. Feuer (1959) has reported a single brood from New Orleans in which some individuals exhibited horizontal and others diagonal bars on the temporal scale. It is the opinion of this investigator that the number and distribution of these intermediate specimens suggests local hybridization rather than the existence of true intergradation. The areas from which the intermediate specimens come have been subject to extensive ecological disturbance as the result of human activities and the relationship between *Storeria dekayi* and *Storeria tropica* may be another example in the growing list of species which undergo some degree of breakdown of reproductive isolation under such conditions. In the New Orleans area specifically, this has been demonstrated in the case of two other species with somewhat similar distributions. Volpe (1960) has reported the common occurrence of hybrids between the toads *Bufo valliceps* and *Bufo fowleri* despite the apparent sterility of all viable hybrids. Evidence of populations of *Storeria* of an intermediate nature existing anywhere along the great extent of ecotone between marsh and higher ground is lacking and it appears that the marsh population is reproductively isolated from *S. d. texana* and *S. d. wrightorum.* This conclusion splits the northern and southern groups of subspecies and necessitates the revival of Cope's name, *Storeria tropica,* for the southern group (Cope, 1885). The marsh population studied here belongs

to the *tropica* group, but is subspecifically distinct from the previously described forms on the basis of the high subcaudal counts and is recognized as a new subspecies under the name *Storeria tropica limnetes* [limnetes, meaning "living in marshes," (Woods, 1944)]. The three subspecies described by Trapido from Mexico, Guatemala, and Honduras were described on the basis of insufficient material and may not all be valid, but adequate numbers of specimens are still not available for a reconsideration of their status at this time. They are therefore retained as subspecies of *Storeria tropica.*

Storeria tropica Cope
Tropical Brown Snakes

Storeria tropica Cope, Proc. Amer. Philos. Soc., vol. 22, p. 175, 1885.
Storeria dekayi tropica Trapido, Amer. Midl. Nat., vol. 31, no. 1, p. 77, 1944.

Holotype.—USNM 6759, collected at Peten, Guatemala, by H. Hague.

Diagnosis.—Distinguished from *Storeria dekayi* by: (1) the absence of dark markings at the corners of the mouth, on the rearmost upper and lower labials; (2) the presence of a horizontal dark line through the long axis of the anterior temporal scale.

Discussion.—*Storeria tropica* as first described by Cope (1885) was considered to be distinct on the basis of the temporal line and the presence of only six supra-labials, rather than the seven characteristic of *Storeria dekayi.* The material now available shows the latter character not to be diagnostic. Labial counts show variation in both species and appear to be particularly variable in the Honduran and Guatemalan populations of *Storeria tropica.* Labial counts range from five to eight in the specimens which are available from this region.

Storeria tropica tropica Cope
Tropical Brown Snake

Storeria tropica Cope, Proc. Amer. Philos. Soc., vol. 22, p. 175, 1885.
Storeria dekayi tropica Trapido, Amer. Mid. Nat., vol. 31, no. 1, p. 77, 1944.

Holotype.—USNM 6759, collected at Peten, Guatemala by H. Hague.

Diagnosis.—This population was distinguished from *Storeria tropica temporalineata* by Trapido on the basis of a lower number of ventral plus subcaudal scales and a "reduced, more pointed snout." With respect to scale counts this diagnosis is slightly misleading since specimens from the range of *S. t. tropica* and from Mexico suggest that the populations represented are identical in subcaudal counts and that the difference in the total count is the result of a tendency toward a lower number of ventral scales in *S. t. tropica.* This subspecies is distinguished from *S. t. anomala* in that it has only two pairs of

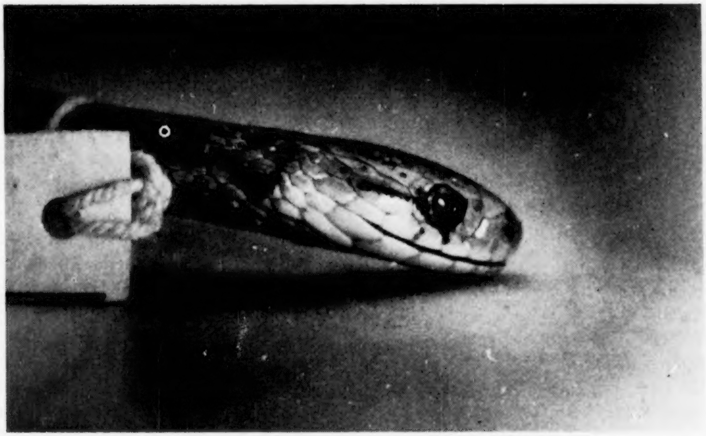

Fig. 4.—*Storeria tropica limnetes* Holotype, TU 11374.

chin shields and from *S. t. limnetes* by lower counts of subcaudal scales.

Specimens examined.—USNM 35921, USNM 6759, MCZ 387146, MCZ 49989, CNHM 20527, CNHM 21796, CNHM 411, AMNH 70208.

Storeria tropica anomala (Dugés)
Orizaba Brown Snake

Storeria dekayi var. *anomala* Dugés, Proc. U.S. Nat. Mus., vol. 11, pp. 9-10, figs., 1888.

Holotype.—Reportedly in Mus. Alfredo Dugés, Univ. Guanajuato, Mexico (Trapido, 1944, Smith and Taylor, 1945).

Diagnosis.—Differs from all other subspecies of *Storeria tropica* in the presence of three pairs of chin shields, rather than two.

Specimens examined.—USNM 5565, USNM 7081, USNM 8939, USNM 110328.

Storeria tropica temporalineata (Trapido) New comb.
Mexican Brown Snake

Storeria dekayi temporalineata Trapido, Amer. Mid. Nat., vol. 31, no. 1, p. 70, 1944.

Holotype.—USNM 32148, collected at San Rafael, Jicaltepec, Veracruz, Mexico by C. H. Thompson.

Diagnosis.—Differs from *Storeria tropica tropica* in having a larger number of ventral scales and from *Storeria tropica limnetes* in having a lower number of subcaudal scales. Distinguished from *Storeria tropica anomala* by the presence of only two pairs of chin shields.

Specimens examined.—USNM 32148, USNM 52300, MCZ 15990, MCZ 2843, UMMZ 99541, UM 85966, KU 23906, AMNH 4292.

Storeria tropica limnetes subsp. nov.
Marsh Brown Snake
Fig. 4

Holotype.—Tulane University Collections 11374, a male collected by Horace Whitten at Waggaman, a settlement south of Harahan, St. Charles Parish, Louisiana on December 2, 1944.

Diagnosis.—Distinct from all other subspecies of *Storeria tropica* in the higher number of subcaudal scales. Differs from *Storeria tropica anomala* in that it has only two pairs of chin shields.

Description of Holotype.—(Fig. 4) Adult male; total length 311 mm, tail length 74 mm; scale rows on body 17 - 17 - 17, ventral scales 134, subcaudals 71, supralabials 7-7, infralabials 7-7, post-oculars 2-2, posterior temporals 2-3, chin shields—2 pairs. Coloration: (in alcohol) Ground color of dorsum Pearl Grey (Maerz and Paul 1950, A-1 in plate 44, page 110), venter Oyster White (Maerz and Paul 1950, B-1 in plate 10, page 43). The dorsal ground color extends over the lateral portions of the ventral scutes so that each has a more or less triangular darker portion on either end where it interdigitates between the dorsal scales of the lowermost row. On the head only the postnasals and 2nd, 5th, 6th and 7th supralabials are immaculate. The 1st supralabials each have a single small dark fleck, while the 3rd and 4th have irregular vertical bars near and parallel to their posterior margins. The internasals, prefrontals, frontal, preoculars, postoculars and parietals all are peppered with dark flecks, increasing in number posteriorly. On the parietals these flecks fuse to form a stripe paralleling the posterolateral edge of each scale. At the junction of the two postoculars there is a fusion of dark flecks to form a blotch behind the eye which is in line with, but not continuous with, the temporal stripe. The temporal line is an irregular black horizontal stripe slightly above the midline of the scale. This line does not quite reach the margin of the scale at either end. On one side both posterior temporals have scattered flecks while on the other side only the dorsal one is so marked. The infralabials and chin shields are immaculate.

A pair of elongate dark spots form an open-ended "V," centered on the dorsal midline of the neck with the wide opening anteriormost. Posterior to this mark there begins a series of paired dark dorsal spots. These tend to fuse to form bars, but only three such bars are complete. The complete bars are located about 1/3 of the body length behind the head. Posterior to this region the spots become smaller and a partially defined lighter median dorsal stripe appears. On the tail, dorsal dark spots are small and mostly confined to the anterior third. Anteriorly, the ventral scales each have 2 to 4 fine dark flecks. These become finer and fewer posteriorly and most of the subcaudals are immaculate. Hemipenis: Terminally there is a crescent-shaped spine-free area. Spines adjacent to this are relatively small. Progressing toward the base the spines become slightly larger. About

1/3 of the way from the base is a zone of large spines. The largest are a pair located dorso-medially and a pair located dorso-laterally. Ventrally there are about 9 definitely enlarged spines in this zone.

Variation.—As was indicated previously, specimens from east Texas have lower subcaudal counts and thus tend to approach *S. t. temporalineata.* In respect to coloration, Trapido's (1944) statement that *temporalineata*-like specimens (those which he designated as intergrades between *temporalineata* and *S. d. texana* and *S. d. wrightorum*) could be recognized by a higher incidence of black markings on the supralabials as compared with specimens of *temporalineata* from Mexico, is unfounded. Four of 7 Mexican specimens of *S. t. temporalineata*, including the holotype, have such marks (57%). Similar markings occur in 31 of 54 specimens of *S. t. limnetes* (also 57%). As is indicated in Figure 2, the number of labials so marked varies from 0 to 5 but there is no indication that *S. t. limnetes* differs from the other populations of *Storeria tropica* in this respect.

Distribution.—*Storeria tropica limnetes* occurs in the salt marshes of the gulf coast of Louisiana and Texas. It is abundant in the Mississippi delta and its eastern limit is apparently Lake Ponchartrain, although it may extend to the mouth of the Pearl River. The western limit of range presently recorded is Galveston Co., Texas.

Habitat.—Within the marshes *S. t. limnetes* may be found under logs and debris on natural levees. Dr. Fred Cagle tells me he has often found individuals in muskrat houses in the open marsh.

Specimens examined.—TU 11374 (holotype). *Topotypic series* from the settlement of Waggaman, Harahan, St. Charles Parish, Louisiana: TU 11570, TU 14063, TU 11893, TU 11762, TU 11762a, TU 11762b, TU 11374a, TU 11374b. *Other specimens examined:* TU 14217, TU 11312, TU 11313, TU 14319, TU 12051, TU 3996, TU 6098, TU 6099, TU 3990-5, TU 3997-8, TU 4001, TU 4003-4, TU 3989, TU 11503, TU 11535, TU 11535a, TU 11535b, TU 11160, TU 7515, TU 14236, TU 7519, TU 6097, TU 10862, TU 11373, TU 6035, UMMZ 86510, MVZ 8162, MVZ 8157, BCB 3883, BCB 4234, REE A-97, REE A-162, USNM 55913, USNM 73828, USNM 15377, USNM 4798a, USNM 5199, USNM 13090.

DISCUSSION

Storeria tropica, if the conclusions of the present study are correct, is a distinct species closely related to *Storeria dekayi.* It is subtropical to tropical in range and in general appears to be a lowland form with mesic requirements. On the basis of the evidence at hand it appears to have diverged from *S. dekayi* or a common ancestor in the southern part of the present range, but a better understanding of the status and distribution of the southern populations of both species is needed before the time and place of differentiation of *Storeria tropica* can be evaluated. The question of the status of *Storeria dekayi victa,* which should be reconsidered in the light of the color pattern resemblance to *S. tropica,* may in turn bear on the history of the latter species.

The disjunction of *Storeria tropica limnetes* from the southern

populations seems, on morphological grounds, to have been of recent occurence. Blair (1958) has interpreted present and past disjunct distributions along the Gulf Costal plain as evidence of Pleistocene cooling. In view of the present distribution of *Storeria tropica,* the existence of populations along the now arid coastal hiatus would require more mesic environments and temperature change need not enter into the problem directly. Blair devotes relatively little attention to the pluvial periods and their significance, but infers from the occurrence of Pleistocene fossils of *Neofiber* in the Texas panhandle and in Kansas, and of Capybaras (*Hydrochoerus* and *Neochoerus*) in Florida, that mesic communities must have existed at some time during the Pleistocene in presently arid areas.

Martin and Harrel (1957), in their discussion of the cloud forest biota of northern Mexico, have concluded that the evidence does not support the occurrence of a cool moist forest corridor during the Pleistocene across the now arid parts of Texas. They suggest, however, that Pleistocene pluvial periods could have resulted in savannah formations and in colonization of expanded river flood plains by mesophytic vegetation. During such intervals of increased stream flow the establishment of marshes or of mesic communities permitting the spread of *Storeria tropica* along the Laguna Madre seems likely. The isolation of Louisiana and East Texas populations was probably initiated in the Hypsithermal, for which Martin (1958) cites the interval between 9,500 and 2,000 years ago.

The sympatry of *Storeria tropica limnetes* and *Storeria dekayi* along the ecotone between the marshes and the communities on higher ground is an inviting problem in the study of isolating mechanisms, particularly in comparison with the situation in the genus *Natrix* in the same area. It may be that both sympatry and hybridization are associated with ecologically disturbed environments. This is an evolutionary pattern which promises to increase in importance in the future.

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Notes and Discussion

"Single-Needled" Loblolly Pine

A loblolly pine (*Pinus taeda* L.) whose fascicles each contain a single, straight, terete needle has been growing for three years in a plantation in eastern Tennessee. Normal trees have 2, 3, or 4 separate and slightly twisted needles in each fascicle.

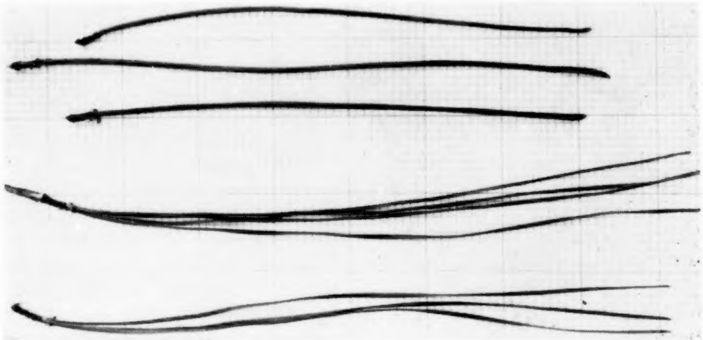

Fig. 1.—Cohering loblolly pine needles at top, normal at bottom.

Each "single needle" consists of 2 to 4 separate ones tightly cohering along their adaxial surface, somewhat similar to a sand pine, *Pinus clausa* (Chapm.) Vasey, reported from Florida (Woods and Dawsey, 1955. *Bot. Gaz.*, 116:292). The component leaves are not cellularly joined but seem held together by some natural adhesive. With care they can be stripped part. From a distance, the tree seems covered with long, green spikes.

Otherwise the tree is normal. The seed-source is unknown. It is one of several thousand loblolly seedlings obtained from the State Nursery at Pinson, Tennessee, and planted at Sewanee in February 1957. No other survivors of the shipment manifest the peculiarity.—T. A. Harrington, Southern Forest Experiment Station, Forest Service, U.S. Department of Agriculture, New Orleans 13, La.

Further Remarks on the Collembolan Genus Hypogastrura with Description of a New Genus

In a previous issue (Yosii, 1960) I discussed the subdivision of the collembolan genus *Hypogastrura* from the chaetotaxical point of view and described certain species. The manuscript was completed and in press, so that I could not refer to the important and interesting notes of Dr. P. Cassagnau (1959). His conclusions parallel mine, but he has recognized *Ceratophysella* as a separate genus from *Hypogastrura*. I regard this change as reasonable and further believe that the subgenus *Cyclograna* (Yosii, 1960) should be elevated to generic rank:

Cyclograna gen. n.

Generic type.—*Hypogastrura vulgaris* Yosii, 1960.

Diagnosis.—Near to *Ceratophysella* Börner 1932. But the accessory tubercle of the postantennal organ is surrounded by two posterior tubercles.

At the same time Cassagnau has divided the genus *Ceratophysella* into two groups: A-type and B-type, which are identical with my *communis*-group and *armata*-group, respectively. His *C. denticulata* (Bagnall) seems to be near to my *C. exilis* (Yosii), although it is not yet certain whether his *C. denticulata* is Bagnall's species, a fact which is not exactly to be determined.

Recent material from the United States in a collection donated by Prof. F. Bonet of Mexico is under study at the moment. In this collection, there are some specimens which are identified as *Ceratophysella pseudarmata* (Folsom). The species which I described under *H. pseudarmata* previously (Yosii, 1960) represents a new species designated as follows:

Ceratophysella brevisensillata sp. n.

Syn.: *Hypogastrura pseudarmata* (nec Folsom) Yosii, 1960.

Diagnosis.—As described in my previous paper (Yosii, 1960: 261, Figs. 4, 24-29).

Holotype.—A male from Arlington, Massachusetts, USA. (15 XI 1950, K. Christiansen).

REFERENCES

CASSAGNAU, P. 1959. Faune française des Collemboles IX, *Les Hypogastrura* du Massif du Néouvielle, Remarques sur la chétotaxie des Espèces. *Vie et Milieu*, **9**:476-503.

YOSII, R. 1960. Studies on the collembolan genus *Hypogastrura*. *Am. Midl. Nat.*, **64**(2):257-281.

—RIOZO YOSII, Yoshida College, Kyoto University, Japan.

Book Reviews

A GATHERING OF SHORE BIRDS. By Henry Marion Hall. Edited and with additions by Roland C. Clement. The Devin-Adair Co., New York. 1960. xii + 242 pp., 95 figs., all pen-and-ink drawings. $10.00.

This book is primarily a series of Hall's articles, many of which have appeared in *Audubon Magazine*. Clement has added to many species accounts and has supplied valuable sections on An Introduction to the Shore Birds, The Shore Bird Families, The South American Shore Birds, and The Wanderers. Clement states that the aim "is to bring Dr. Hall's essays up to date in a series of comments on recent changes of status which have occurred, and to interpolate some of the more readable scientific commentaries gleaned from a perusal of an extensive literature in order to introduce the non-professional reader to a particularly attractive group of birds." This objective has been attained.

Readable and interesting individual accounts of "57 Shore Birds Breeding in North America" north of the Panama Canal comprise 202 pages. Habits, habitats, plumages, field marks, behavior, local names, and ranges are discussed for each species. Hall has based many of his observations on experiences along the Atlantic coast, where he has hunted and observed shorebirds. Clement's contributions improve and round out this section. Emphasis is placed on the increase of shorebirds after they were protected from hunting. Lay readers will enjoy the section on South American shorebirds and the lists of North American species which share their ranges with South America, Europe, and Asia. Except for that of the dead Eskimo Curlew (p. 11), most of the line drawings by John Henry Dick are pleasing and add to the book.

Of the "breeding" species discussed in some detail, the Ruff and Curlew Sandpiper are not known to nest in North America. I found many of the local names of shorebirds unfamiliar and confusing when used interchangeably in the text. There are minor inconsistencies in the usage of "accepted" vernacular names — "Hudsonian Whimbrel," "Whimbrel," or "Hudsonian Curlew" for Whimbrel; "Wilson's Snipe," "Wilson's Common Snipe," and "Common Snipe" for the latter; "Tatler" and "Tattler," each repeated several times. Banding studies have not substantiated that Black Oystercatchers "mate for life" (p. 34). One doubts that American Woodcocks can be sexed upon flushing (p. 85) or that Black-bellied Plover tracks are larger than those of the Ruffed Grouse (p. 67).

Under "American Shore Birds in Europe," the American Avocet is included because it is accidental in Greenland, but under "European Shore Birds in America," the European Oystercatcher, Eurasian Golden Plover, and Redshank are listed only because *they* occur in Greenland.

All of these minor criticisms do not detract greatly from the value of the volume, and those for whom it is intended will find much informative and enjoyable reading in it.—RUSSELL E. MUMFORD, Purdue University, Lafayette.

ECOLOGY OF INLAND WATERS AND ESTUARIES. By George K. Reid. Reinhold Publishing Corp., New York. xi + 375 pp., 100 figs., 12 tables. 1961. $7.50.

Flowing waters have been neglected in limnology texts. Dr. Reid's book attempts to present a balanced treatment of both lakes and streams as well

as estuaries. Part I considers physiography and sediments; Part II, water and its properties; Part III, light, heat, hydrography, dissolved gases, and solids; Part IV, aquatic organisms, discussed in phylogenetic sequence; and Part V, populations and aquatic communities. The selection of subject matter and the relative attention given the various disciplines is satisfactory. Biogeography, evolution, and problems of species abundance are mentioned only incidentally. The floristic and faunistic survey is restricted to the United States, with a few exceptions.

The book is written for undergraduate students with little scientific background, so that much of the text is devoted to explaining elementary facts and principles of geology, physics, chemistry, and biology. Furthermore, citations to the bibliography (which is adequate) are seldom given in the body of the text. These two features render the book unsuitable for advanced students or as a reference for applied limnologists.

Although Reid's prose will make the purist cringe, the sentences are short and crisp, and usually readily understandable. Poor definitions and errors of fact are too numerous; e.g., "discharge" and "potential natality" are incorrectly defined; the freshwater mysid, *Taphromysis*, is overlooked, and *Craspedacusta* is said to have been introduced from South America or the West Indies.

The physical makeup is attractive and the figures are good. The instructor who is courageous enough to teach limnology at the sophomore or junior level will find this text useful.—ALFRED E. SMALLEY, Tulane University, New Orleans, Louisiana.

LIVINGSTONE'S PRIVATE JOURNALS 1851-1853. Edited by I. Schapera. University of California Press, Berkeley and Los Angeles. XXIV — 341 pages, including 3 maps. 1960. $5.00.

This is the first complete publication of Livingstone's records of two journeys to Northern Rhodesia only slightly more than a century ago. For anyone interested in historical data for purposes of evaluating the biological changes that have taken place in Africa in so short a segment of history, Livingstone's records are essential and usually engagingly written.

Although the name of Livingstone is associated with missionary activities in Africa, these journals amply testify that he was also an adventurous naturalist and explorer, so much so that the intrusion of gospel moralizing is excusable. Although Livingstone's own observations on plants and animals are excellent, his deductions are often influenced by the knowledge of his times thus providing the reader with an extra dividend of historical value. His account of the biology of the tsetse fly and its distribution is of great interest and so also are his observations on the "bullfrog"; tree rings of the baobab and its age; bushman arrow poison and the eastwardly distribution of these people; hornbill nesting habits, probably the first to be published; the wide-spread use of *Cannabis sativa;* termite flights; and the habits of the tick bird.

Of great interest are his medical comments; his credulity with respect to native folklore; his criticism of native superstitions that differ so little from some of his own; and his comment on the approaching "Golden Age" of civilization; and his use of "alligator" for crocodile, and "tiger" for leopard, usage that one still encounters among nontechnical people.—R. B. COWLES, University of California, Los Angeles.

PRINCIPLES OF ANIMAL TAXONOMY. By George Gaylord Simpson. Columbia University Press, New York, N. Y. 247 p., 1961. $6.00.

Professor Simpson states categorically that the title of this book is to be taken literally. "The subject is principles, and particular groups of organisms or classifications thereof are involved only as examples and as the basis for inductive derivation of principles. The principles are those of taxonomy, as strictly defined hereinafter. . . . The kind of taxonomy involved is explicitly that applicable to animals, by which I mean metazoans. Most of the same principles apply to plants and many of them, with less generality, to protists. Although such applications may be mentioned in passing, they are largely incidental. Examples are drawn principally from mammals, for personal and practical reasons. Principles derived from and applicable to mammals are sufficiently general from all Metazoa that the word 'animal' in the title should not constitute false advertising, but a specialist in, say, coelenterates may quite properly reach some other conclusions in the light of his different experience."

The reviewer, a taxonomic botanist, having duly noted in the introductory paragraphs that most of the principles apply to plants, soon wished that the author had been less modest, had eliminated the word "animal" from the title, and had not cared a hoot about advertising one way or the other. Were the reader, if a botanist, to cross in his mind's eye the word "animal" from the title, to substitute in the text in appropriate places the word "plant" for "animal," the word "botanical" for "zoological," etc., he could scarcely wish for a better discussion of the principles pertinent to taxonomic botany. My comments, then, relate to the particular value the book seems to me to have for botanists.

As a teacher-student of plant taxonomy, I have often wished for a comprehensive, unified treatise on taxonomic principles. One can, of course, read (and have his more advanced students read) numerous shorter essays and various papers and books which one way or another elucidate certain of the taxonomic principles. This, however desirable in a complimentary fashion, is no satisfactory substitute for a searching, lucid, coherent exposition of the principles in an over-all context. There are botanical textbooks of relatively recent vintage having the word "taxonomy" in their titles. None of these books is primarily about taxonomy in the sense of Simpson (see p. 11). Certainly their authors purport to treat taxonomic principles, among other things, but one is hard put to it to divine what precisely it is they consider those principles to be.

Not the least service done by Simpson in his book is that of establishing precisely what is meant (at least by him) by systematics, taxonomy, classification, and nomenclature. It would seem that these terms, so commonly employed, so basic to communication in biology, would hardly require a full chapter for their proper definition. The hash that has, in general, been made with them is only exceeded by (thank goodness!) the clarity with which they are here ordered. This logical general terminology, if adopted and not quibbled over, has much virtue.

The history of classification and of taxonomy is more often than not presented as a dry, dull detailing of significant milestones or of the names of significant persons, their birth dates and death dates, and a few dusty driblets as to their contributions. Simpson with refreshingly uncommon facility reviews the history of concepts, ideas, and systems pertinent to the historical origins of and development of current taxonomic thought.

The author's ambitious objectives include examination of the "deepest

foundations" of taxonomy and the hope that students may be provided with rudiments with which to learn to think about taxonomy and not just to do it. His well integrated discussions comprise an eminently successful achievement of these purposes. And the web is so nicely woven it seems hazardous to single out some threads for examination.

In view of the many prior disputations regarding the species concept, and despite recent relative agreement on a so-called "biological" or genetical concept, the section on the species and lower categories has much to offer in the way of a rational appraisal. For those of us (perhaps mostly botanists) who have objected to dependence on the single criterion of interbreeding (or lack of it) in formulation of a definition, the cockles of our hearts are tickled by: "Species do evolve, and almost always do so gradually. Among evolutionary species there cannot possibly be a general dichotomy between free interbreeding and no interbreeding. . . . To insist on an absolute objective criterion would be to deny the facts of life, especially the inescapable fact of evolution." Elsewhere (p. 110) Simpson says that a basic principle of taxonomy is that its results should be useful. If recognition of species as such has any value in biological communication, then of necessity a flexible concept must be derived from the somewhat less than static facts of life. In these regards there is an illuminating discussion apropos of species in uniparental organisms. One can but wish that apomixis of the variety of kinds known in plants occurred also in animals so that we might have the benefit of Simpson's critical analysis on this too.

This book will provide the teacher of a course in taxonomy, animal or plant, wherein it is neither desired nor intended that his students merely perform exercises in identification or limited classification, a stimulating, thought-provoking, and comprehensive discussion of the theoretical bases, principles, procedures, and rules of the subject. Suitable examples can readily be provided by the instructor from his own different experience with which to illustrate.

This book is sufficiently free of jargon so that the reader need not become afflicted with hardening of the categories.—R. K. GODFREY, Department of Biological Sciences, Florida State University.

Books Received

A SURVEY OF VARIOUS LATE CENOZOIC VERTEBRATE FAUNAS OF THE PANHANDLE OF TEXAS. Part III. Felidae. By Donald E. Savage. University of California Press. 28 p., 7 text figs. 1960.

STRATIGRAPHY AND PALEONTOLOGY OF THE PERMIAN NOSONI AND DEKKAS FORMATIONS (BOLLIBOKKA GROUP). By Alan H. Coogan. University of California Press. (Univ. Calif. Publ. Geol. Sci., 36(5):243-316, 5 pls., 23 text figs.). 1960. $1.75.

A MARINE CARNIVORE FROM THE CLALLAM MIOCENE FORMATION WASHINGTON. By R. A. Stirton. University of California Press. (Univ. Calif. Publ. Geol. Sci., 36(7):345-368, 4 text figs.). 1960. $0.75.

GUIDE TO THE STUDY OF THE ANATOMY OF THE SHARK, NECTURUS, AND THE CAT. 3rd ed. By Samuel Eddy, Clarence P. Oliver and John P. Turner. John Wiley & Sons, Inc., New York. viii + 141 p. 1960. $3.50.

THE MECHANISM OF EVOLUTION. By W. H. Dowdeswell. Harper Torchbooks: The Science Library. Harper and Brothers, New York. 115 p. 1960. $0.95.

MOLLUSCS. By J. E. Morton. Harper Torchbooks: The Science Library. Harper and Brothers, New York. 232 p. 1960. $1.40.

NATURAL SELECTION AND HEREDITY. By P. M. Sheppard. Harper Torchbooks: The Science Library. Harper and Brothers, New York. 209 p. 1960. $1.35.

LATE PLIOCENE FLORAS EAST OF THE SIERRA NEVADA. By Daniel I. Axelrod and William S. Ting. University of California Press. (Univ. Calif. Publ. Geol. Sci., 39(1):1-118, pls. 1-24, 10 text figs.). 1960. $2.50.

MULTIVARIATE ANALYSIS OF PLEISTOCENE AND RECENT COYOTES (CANIS LATRANS) FROM CALIFORNIA. By Eugene Giles. University of California Press. (Univ. Calif. Publ. Geol. Sci., 36(8):369-390, 4 text figs.). 1960. $0.75.

MISSISSIPPIAN AND DEVONIAN PALEONTOLOGY AND STRATIGRAPHY QUARTZ SPRING AREA, INYO COUNTY, CALIFORNIA. By R. L. Langinheim, Jr. and Herbert Tischler. University of California Press. (Univ. Calif. Publ. Geol. Sci., 38(2):89-152, 1 pl., 18 text figs.). 1960. $1.25.

DISPLACED MIOCENE MOLLUSCAN PROVINCES ALONG THE SAN ANDREAS FAULT, CALIFORNIA. By Clarence A. Hall, Jr. University of California Press. (Univ. Calif. Publ. Geol. Sci., 34(6):281-308, 1 chart, 3 maps). 1960. $1.25.

OLIGOCENE PLANTS FROM THE UPPER RUBY RIVER BASIN, SOUTHWESTERN MONTANA. By Herman F. Becker. The Geological Society of America, Memoir 82. 127 p. 32 pls. 1961.

THE MONARCH BUTTERFLY. By F. A. Urquhart. University of Toronto Press, Toronto. 361 p. 79 figs., 12 plates. 1960. $6.50 cloth; $3.95 paper.

HERBICIDES AND THE SOIL. Edited by E. K. Woodford and G. R. Sagar. Blackwell Scientific Publications, Oxford. 88 p. 1961. $3.50.

THE AMATEUR SCIENTIST. By C. L. Strong. Introduction by Vannevar Bush. Simon and Schuster, New York. 584 p., 256 text figs. 1960. $5.95.

SCIENTIFIC WORDS: THEIR STRUCTURE AND MEANING. By Dr. W. E. Flood. Duell, Sloan and Pearce, New York. 220 p. 1960. $3.50.

THE RELATIONSHIP OF THE PEARY AND BARREN GROUND CARIBOU. By T. H. Manning. Arctic Institute of North America, Technical Paper No. 4. 52 p., 9 figs. 1960. $2.00.

MARINE INFAUNAL BENTHOS IN ARCTIC NORTH AMERICA. By Derek V. Ellis. Arctic Institute of North America, Technical Paper No. 5. 53 p. 17 figs. 1960. $2.00.

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